AN ABSTRACT OF THE DISSERTATION OF

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Abstract approved:____
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Recent climatic warming trends and increases in the frequency and extent of wildfires have prompted much concern regarding the potential for rapid change in the structure and function of forested ecosystems around the world. Episodes of mortality in wildfires and insect outbreaks associated with drought have affected large areas and altered landscapes, but little is known about the cumulative effects of these disturbances at the regional scales. I used data from two different forest inventories in the Pacific Northwest to develop a framework for tracking regional forest dynamics and examine variation in tree mortality rates among vegetation zones that differ in biophysical setting as well as recent and historical disturbance regimes.

In the second chapter I developed an empirically based framework for tracking regional forest dynamics using regional inventory data collected from 2001 to 2010. I characterized the major dimensions of forest structure and developed a classification incorporating multiple attributes of forest structure including biomass, size, and density of live trees, the distribution and abundance of dead wood, and the cover of understory vegetation. A single dimension related to live tree biomass accounted for almost half of the variation in a principal components analysis of structural attributes, but dimensions related to density and size of live trees, dead wood, and understory vegetation accounted for as much additional variation. Snags and biomass of dead and downed wood were related to multiple dimensions while understory vegetation acted independent of other dimensions. Results indicated that structural development is more complex than a monotonic accumulation of live biomass and that some components act independently or emerge at multiple stages of structural development. The hierarchical classification reduced the data into three “groups” based on live tree biomass, followed by eleven “classes” that varied in density and size of live trees, and finally twenty-five structural types that differed further in the abundance of dead wood and cover of understory vegetation. Most structural types were geographically widespread but varied in age of dominant trees by vegetation zone indicating that similar structural conditions developed in environments with different biophysical setting, climate, and disturbance/successional histories. Low live biomass structural types (<25 Mg/ha) differed in live tree density and the abundance of live and dead legacies, demonstrating that the variation in early developmental stages depends on the rate of tree establishment and the nature and severity of recent disturbance. Forests in early developmental stages made up less than 20% of most vegetation zones and diverse types with live or dead legacies associated with wildfires were rare. Moderate live biomass structural types (25-99 Mg/ha) represented multiple mid, mature, and late developmental stages, some of which lack analogs in existing conceptual models of structural development such as lower density woodlands with big trees. These structural types included two that have high densities of snags indicative of recent episodes of mortality; together these made up as much as 10%

of some dry vegetation zones. Several high live biomass structural types (100->300 Mg/ha) were identified and substantiated the diversity and relative dominance of mature and later developmental stages, particularly in wet vegetation zones. The relative abundance and make up of structural types varied widely by vegetation zone. Most forests in wet vegetation zones had moderate to high live biomass and were in mid and mature developmental stages, while diverse early developmental stage stages were extremely rare. Dry forests had a far greater range of variation in the relative abundance of structural types which is partially attributable to the greater range of climatic conditions they included, but also to the occurrence of recent episodes of mortality associated with wildfires and insects.

In the third chapter I examined variation in tree mortality rates using a different regional inventory that occurred from the mid-1990s to the mid-2000s. I compared the distribution of rates among stands in different vegetation zones and stages of structural developmental. I developed a simple framework based on changes in live tree density and mean tree size and examined trends in structural change associated with disturbances at different levels of mortality across all stages of structural development. Most plots were within the range of "background" mortality rates reported in other studies (<1.0 %/yr) and extremely high "stand-replacing" levels of mortality (≥25%/yr) were rare. Approximately 30% of plot mortality rates occurred at intermediate levels (>1%/yr and <25%/yr) as result of insects and fire, highlighting the importance of conceptualizing mortality as a continuum as opposed to just "background" or "stand-replacement" to fully represent dynamics at a regional scale. The distributions of mortality differed among many vegetation zones. Levels of mortality were primarily <2.5%/yr in western

hemlock, silver fir, and mountain hemlock vegetation zones where fires were rare and insects and pathogens occurred predominantly at endemic levels. Rates were highest in subalpine forests and higher elevation grand fir and Douglas-fir forests as a result of fire and insects. Mortality rates in ponderosa pine, the hottest driest forest vegetation zone, were surprisingly low, and there was little to no mortality in plots with no evidence of disturbance. Mortality rates varied among developmental stages in all vegetation zones but few consistent patterns emerged. Levels of mortality were often lowest in early developmental stages but varied in later stages where they were lowest in wet vegetation zones and highest in subalpine and dry vegetation zones. Application of a simple framework indicated that multiple trajectories of structural change were common at levels of mortality <2.5%/yr, but structural change at higher levels was predominantly associated with a "thinning" trajectory defined by decreases in density and increases in mean tree size. Results indicated that the rate and magnitude of mortality related change during the study period varies widely across the region. Rapid change has occurred in subalpine, grand fir/white fir, Douglas-fir, and ponderosa pine vegetation zones where disturbances such as insects and fire were widespread. However, these disturbances have potentially restored some aspects of historical structure by reducing overall density and increasing the dominance of bigger trees. In western hemlock, silver fir, and mountain hemlock vegetation zones where higher levels of mortality related to disturbances were rare, wildfires have increased landscape diversity by creating diverse early successional habitats and most change was more subtle but may be manifest oevr longer periods if current trends continue. This examination of short-period mortality rates and associated structural change across a broad geographic provides context for understanding trends

from localized studies and potential ecological consequences of mortality, but there is still a great deal of uncertainty as to how the effects of a changing climate and disturbance regimes will manifest themselves over longer time scales.

This dissertation is one of the first field based assessments of recent forest dynamics at a regional scale. The results of both chapters, each based on a different dataset, told a similar story. The abundance of structural types in various vegetation zones estimated during the mid-2000s was consistent with the cumulative effects of tree mortality during the preceding decade. It was evident that wildfire effects and recent mortality were small relative to the regional extent of the study and have contributed to structural diversity and restoration of historic structure in stands where fire exclusion and past logging has increased total stand density and decreased the dominance of big trees. However, the rate of change and cumulative effects of recent forest dynamics varied widely by geographic location and vegetation zone and there was greater variability and uncertainty regarding the effects of mortality at smaller landscape scales where individual events like large wildfires have the potential to rapidly alter the landscape structure and composition. Assessing this variability and the scales at which trade-offs (e.g. losses of old-growth and creation of diverse early developmental stages) occur will be an important next step in understanding the cumulative ecological effects of recent wildfires and tree mortality on Pacific Northwest forests.

Contemporary Regional Forest Dynamics in the Pacific Northwest

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Matthew J. Reilly

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Matthew J. Reilly, Author

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Thomas A. Spies was involved with review and interpretation of results as well as extensive review and editorial suggestions for Chapters 2 and 3. Committee members Patricia Muir and David L. Peterson gave detailed reviews and editorial suggestions for Chapter 2, as did Janet L. Ohmann, Raymond J. Davis, and Julia I. Burton. Matthew J. Gregory and Heather M. Roberts provided plot level data summaries used in both Chapter 2 and 3.

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DEDICATION

To the memory of my grandfather, Louis Gaetano DiRusso (1929-2012).

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Chapter 1: Introduction

A rapidly changing climate is expected to significantly alter the structure and function of forested ecosystems around the world (Vose et al. 2013). Climate change has already been implicated in increasing rates of tree mortality (van Mantgem et al. 2009), regional scale vegetation die-off (Breashears et al. 2005, Allen et al. 2010, Williams et al. 2010, Carnicier et al. 2011), widespread outbreaks of insects and pathogens (Raffa et al 2008), and an increase in the frequency and extent of wildfires (Westerling et al 2006, Littell et al. 2009). However, despite a growing awareness and concern regarding the effects of recent disturbance and mortality, few studies have actually investigated the patterns and consequences of mortality and recent forest change in an ecological context (Anderegg et al. 2012). Several studies have focused on individual vegetation zones in specific geographic subregions (Allen et al. 2010, Carnicier et al. 2011, Williams et al. 2010, Luo and Chen 2013) or on individual stages of development (e.g. old-growth) (van Mantgem et al 2009, Moeur et al. 2011), but few if any have done regional scale assessments that include forests in all developmental stages and multiple vegetation zones occurring in different biophysical settings with variable recent and historical disturbance regimes. How has the amount of forest in different developmental stages changed? How has recent mortality changed stand structure? Do these changes differ among vegetation zones? Answers to questions such as these can enhance our understanding of the cumulative effects of recent forest change as well as our knowledge regarding how the role of tree mortality in stand dynamics and structural development varies among vegetation zones.

Poor understanding of the cumulative effects of recent episodes of mortality is partially due to the lack of a large datasets and a framework with which to track change across a regional extent with multiple vegetation zones that differ in biophysical setting and recent and historical disturbance regimes. Much of our current conceptualization of variation in forest structure has come from studies focused on the development of structural complexity in old-growth forests following stand replacing disturbances such as wildfire and logging (e.g. Oliver and Larson 1990, Franklin et al. 2002). These models offer a linear approach to structural development where specific stages are defined by the processes occurring during each stage (e.g. stand initiation/reorganization, stem exclusion/self-thinning, understory re-initiation/ maturation, old-growth). Although these models are useful in many forests subject to infrequent, stand replacing disturbances, they are insufficient to encompass the full range of structural states present in forests subject to non-stand replacing disturbances where multiple, non-linear developmental pathways are possible (Frelich 2002). In order to understand forest dynamics across broad spatial scales encompassing broad productivity gradients and multiple vegetation zones with diverse disturbance regimes, a more generalizable classification system capable of tracking structural change at stand and regional scales is needed (O'Hara et al 1996, Hessburg et al. 2000).

Additional uncertainty surrounding recent forest dynamics is also due to a limited understanding of the actual variation in mortality rates during a given period and how mortality as a demographic process may be manifest in structural change. Tree mortality is often conceptualized as "background mortality" in undisturbed forests which refers to low, relatively stable rates of mortality associated with endogenous fine-scale processes such as density dependent thinning, resulting from competition for resources or senescence of older trees (Chen et al. 2008). Despite its usefulness as a baseline with which to compare future changes, the concept of background mortality is insufficient to represent variation in tree mortality across larger spatial scales where a variety of natural disturbances may be operating (Lugo and Scatena 1996, Vanderwel et al. 2013). At the other end of the spectrum, mortality is often considered "catastrophic" and indicative of stand-replacing disturbance (Lugo and Scatena 1996). However, though some mortality resulting from disturbance may be stand-replacing, mortality from drought and disturbance often operates across a range of levels which can result in a variety of changes in forest structure depending on the agent of disturbance (Elliott and Swank 1994, Allen and Breashears 1998, Mueller et al. 2005). Recent work indicates that background mortality rates are increasing in both temperate and tropical forests (Gentry and Phillips 1994, Phillips et al. 2004, van Mantgem et al 2009, Peng et al. 2011), but there is much uncertainty and confusion distinguishing between the effects of mortality associated with stand development processes and those associated with exogenous stress induced by climate (van Mantgem et al 2009, Peng et al. 2011, Luo and Chen 2013). Likewise, reducing mortality in disturbances like wildfires to a few levels of severity limits understanding of the actual structural change that occurred. Understanding the distribution of mortality rates across a region and associated structural changes at different levels of mortality can complement remote sensing based studies and can likely enhance resolution regarding the ecological effects of mortality.

Previous studies of forest dynamics at large regional scales have traditionally been conducted at correspondingly long times scales (Delcourt et al. 1983, Delcourt and Delcourt 1988). However, recent studies suggest the potential for rapid changes in vegetation structure from mortality at decadal or even annual temporal scales to have profound effects at large spatial scales (Allen and Breshears 1998, Breshears et al. 2005, Carnicer et al. 2011). Models indicate the future potential for widespread changes in vegetation structure based on various climate scenarios (Westerling et al. 2011, Wiiliams et al. 2013), but there is still limited understanding of the rate and magnitude of recent change and the associated cumulative ecological effects of recent mortality and disturbance. Wildfires and other disturbances play a very important role in the development of structural complexity (Franklin et al. 2002) and can play ecologically beneficial roles by restoring forest structure, and creating wildlife habitat, but common perceptions currently driving policy on federal forests (e.g. The Healthy Forest Initiative) often regard their effects as “detrimental” or “catastrophic”. Forests of the Pacific Northwest have seen large increases in background mortality rates (van Mantgem et al. 2009) and the area affected by wildfire (Littell et al. 2009) and insects (Meigs et al. 2011), but the cumulative effects of these changes on forest dynamics relating to trends in structural development or the abundance of different developmental stages have yet to be quantified and a comprehensive retrospective analysis is needed.

Fire was one of the primary drivers of historical forest dynamics in the Pacific Northwest (Agee 1993). Frequency and severity differed spatially and temporally and determined the historical range of variation in stand structure and the relative abundance of forests in different stages of structural development (Wimberly et al. 2000, Agee 2003). Fire regimes varied across the region and ranged from high frequency, low and mixed severity regimes in drier vegetation zones (Wright and Agee 2004, Taylor and Skinner 2003, Heyerdahl et al. 2001) to lower frequency, higher severity regimes in wet and cold vegetation zones (Hemstrom and Franklin 1982, Weisburg and Swanson 2003). The prevalence of fire exhibited temporal oscillations on the scale of centuries and millenia**,** with the synchronous occurrence of fires across the region during some periods and other periods experiencing less widespread fire (Cwynar 1987, Weisburg and Swanson 2003, Colombaroli and Gavin 2010).

Forest dynamics during the 20th century were driven mostly by a variety of anthropogenic influences which varied across the region affecting the abundance of forests in different successional states. Forests in the drier vegetation zones of the region were directly affected by grazing of domestic animals and large wildfires associated with industrial scale logging and settlement around the turn of the century. Post-settlement forest dynamics were then driven by clearcutting and high grading of remnant old-growth ponderosa pine (*Pinus ponderosa*) as well as the indirect effects of fire exclusion. Fire exclusion in drier forests enabled the establishment of multiple cohorts of shade tolerant but fire intolerant trees during the 20th century (Youngblood et al. 2004, Merschel et al. 2014). As a result it is hypothesized that stand density has increased greatly in places where fires were historically most frequent, thus decreasing landscape diversity by homogenizing stand structure at the landscape and regional scale (Perry et al. 2011). The effects of fire exclusion are greatest in drier forests where old-growth structure has shifted with high density in the midstory (Camp 1999, Youngblood et al. 2004). Fire exclusion has had less of an effect on forests where historic return intervals were longer (Noss et al. 2006), particularly at higher elevations and in the moister and colder vegetation types. Despite efforts to suppress wildfire that began in the early part of the 20th century, several high severity wildfires associated with slash burning affected large areas as late as the 1940's.

Industrial scale logging also started at the end of the 19th century across the region. Logging reached its peak on federal lands in the latter half of the century following World War II in the 1950's when much of the old-growth in the region was harvested until the passage of the Northwest Forest Plan (NWFP) in 1994 (USDA and USDI 1994). Passage of the NWFP created a network of late successional reserves around the region in order to provide habitat for the endangered Northern Spotted Owl (*Strix occidentalis*) and greatly reduced harvesting on federal land. Regenerating clearcuts from a period of industrial logging have since gone through canopy closure while stands that established earlier in the century from logging and fires are currently maturing and beginning to develop old-growth characteristics.

Like many regions around the world, the Pacific Northwest has recently experienced extreme drought (Schwalm et al. 2012), increases background mortality rates of trees of old-growth forests (van Mantgem et al. 2009) and an increase in area burned by wildfire (Littell et al. 2009) with the occurrence of multiple extremely large events in the last few decades. Despite some research on recent wildfires across the region (Larson and Franklin 2005, Thompson et al. 2007, Prichard et al. 2010, see Halofsky et al. 2011 for review), no one has examined the cumulative ecological effects of contemporary wildfires and put these effects in the context of regional forest structure and dynamics. Thus far, the few landscape level studies of wildfires in the Pacific Northwest have focused explicitly on the drivers (Thompson and Spies 2009, Thompson and Spies 2010) and spatial patterns of severity (Cansler 2011) as opposed to actual ecological effects of wildfire and there is little knowledge on how wildfires have affected the abundance of habitats at regional scales with the exception of late successional and old-growth forests (Mouer et al. 2011, Ohmann et al. 2012, Davis et al. *In Review*). Although loss of Northern Spotted Owl habitat has been a primary concern (Spies et al. 2006), there is growing awareness and recognition of the importance of early successional post-fire habitats following high severity fire (Hutto 2008). What are the cumulative effects of succession, wildfires, and other disturbances on the relative abundance amounts of old-growth and diverse early successional forests?

This dissertation examined the cumulative effects of recent dynamics in the forests of the Pacific Northwest and assessed the extent of recent mortality as well as the magnitude and direction of stand-level structural change. How much of the region has been affected by various levels of tree mortality? Are the corresponding trajectories of structural change toward earlier or later development stages? Although some studies have been conducted on individual fires or insect outbreaks, there is little understanding of the cumulative ecological effects of these disturbances at the regional scale or how they differ among vegetation types across the region. In order to understand the cumulative effects of mortality and disturbance, there is a need to consider their effects in the context of undisturbed forests. Individual disturbance events may result in drastic ecological change at landscape scales, but assessing the effects of these in the context of undisturbed forests will provide a better understanding of the overall stability of forests in the Pacific Northwest during a period of time characterized by widespread fire, insect outbreaks, and extreme drought.

In the second chapter of this dissertation I develop an empirically based framework for tracking regional forest dynamics based on multiple dimension of forest structure including the abundance, size and density of live trees, the abundance of snags and downed wood, and the cover of understory vegetation. The framework can be used to assess the cumulative effects of mortality associated with recent and historical disturbance and serve as a baseline with which to compare future change across the region. The third chapter examines regional variation in tree mortality rates and structural development. I compare distributions of tree mortality rates across the Pacific Northwest and characterize structural change using a simple framework based on changes in density of live trees and average tree size. Examining the distribution of mortality rates allows for the comparison of the extent, magnitude, and direction of structural change assess the potential variability in short term responses among the major vegetation types in the Pacific Northwest. In the fourth and final chapter, I summarize my findings and discuss management implications, broader impacts, and final conclusions on late 20th/early 21st century regional forest dynamics in the Pacific Northwest.

Chapter 2: Regional variation in forest structure in Oregon, Washington, and Northern California, USA

Abstract

Despite the importance of forest structure to biodiversity and ecosystem function, regional scale variation across multiple forest types is poorly understood. I characterize the major dimensions of forest structure, develop an empirically based classification of structural types, and compare the composition of types among vegetation zones across 25 million ha of forest using over 11,000 plots from all ownerships in the Pacific Northwest, USA. A single dimension related to live tree biomass accounted for almost half of the variation in a principal components analysis of structural attributes, but dimensions related to density and size of live trees, dead wood, and understory vegetation acFinney counted for as much additional variation. Snags and biomass of dead and downed wood were related to multiple dimensions while understory vegetation acted independent of other dimensions. Results indicate that structural development is more complex than a monotonic accumulation of live biomass and that some components act independently or emerge at multiple stages of structural development. Low live biomass structural types (<25 Mg/ha) representative of early seral forests demonstrate the potential variation in live and dead legacies and persistence of early developmental stages. Moderate live biomass structural types (25-99 Mg/ha) represent multiple developmental stages. Those associated with past logging or aggradation from meadows, grasslands, and shrublands lacked dead wood, but some less common types resulting from non-stand replacing disturbance were rich in live and dead legacies. High live biomass structural types (>100

Mg/ha) exhibited considerable variation in the abundance of dead wood and big trees and substantiated the diversity of later developmental stages. Age differed among structural types in most wet forests, but overlapped considerably in dry forests. Wet forests were dominated by mature and later developmental structural types and diverse early seral types were extremely rare. Dry forests had greater variation in the composition of structural types where woodland types were common and recent wildfires have created diverse early seral types. This analysis provides a framework for conceptualizing and understanding regional forest dynamics and uncovers structural relationships, stages, and patterns that both support and challenge existing conceptual models of forest development and regional assessments of forest conditions.

Key Words: structural development, early seral vegetation, old-growth, live and dead biomass, understory vegetation, tree density and size, wildfire, logging, disturbance history

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Introduction

Despite the importance of forest structure to ecosystem function (Waring and Running 2007) and biodiversity (MacArthur and MacArthur 1961), regional scale variation in forest structure is poorly understood. Past large scale studies have focused primarily on how climate constrains biomass (Gholz 1982, Malhi et al. 2006, Urquiza-Haas et al. 2007, Hudiburg et al. 2009), but more detailed investigations of other attributes of structure such as snags and dead or downed wood are rare (Spies and Franklin 1991, Ohmann and Waddell 2002, Ohmann et al. 2007, Ares et al. 2012). Although structural development has been conceptualized for a few well-studied forest types (Bormann and Likens 1979, Oliver and Larson 1990, Franklin et al. 2002, Frelich 2002), we lack a conceptually or empirically based biogeographic understanding of how variation in the distribution of live and dead biomass results in different structural types across very large spatial extents (>100,000 ha) where climate, disturbance regimes, and species composition differ.

Vegetation structure can be broadly defined as the vertical and horizontal distribution of live and dead vegetation (Spies 1998). In most temperate forested ecosystems, structure can be broken down into three major components including live trees, dead wood, and non-arborescent understory plants (Franklin et al. 2002). The live tree component is the most commonly studied component of forest structure and is often described using simple metrics (e.g. biomass, basal area, tree density) as well as variation in size and spatial arrangement of trees (e.g. Pommerening 2002). The dead wood component can be broken down into number and size of dead standing trees (snags) and (coarse woody debris). Snag abundance is often quantified by density (per unit area), but because dead wood is continually breaking down through fragmentation and decomposition, volume or biomass estimates offer more precise estimates on the abundance of snags and coarse woody debris in ecosystem studies (Harmon et al. 1986). Understory vegetation can be further characterized into functional groups (e.g. forbs, shrubs, graminoids) and is generally quantified with estimates of cover or biomass. All three components are intimately linked as the cumulative result of the processes of growth, mortality, and decomposition (Spies 1998). As a result, forest structure is an inherently complex multivariate concept with broad ecological implications that vary by individual components and ecological context.

Much of our current conceptualization of structural variation at the stand scale (1-100 ha) has focused on structural development following stand replacing disturbances such as wildfire and logging (Bormann and Likens 1979, Oliver and Larson 1990, Franklin et al. 2002). These conceptual models offer a linear age and/or process based approach to stand development. Ordered stages are represented by a single pathway along which unique structural conditions result from the dominant processes occurring during each stage (e.g. stand initiation/ reorganization, stem exclusion/self-thinning, understory re-initiation/ maturation, old-growth). Forest structure may be simple or diverse/complex during early developmental stages depending on the disturbance and presence of biological legacies such as large live trees, snags, and downed wood (Franklin et al. 2002, Swanson et al. 2010, Donato et al. 2012). Structure during mid-developmental stages is generally conceived as less diverse as live trees are typically dominated by a single cohort and the dead wood and snags created by stand replacement disturbances have largely decomposed. Structural diversity increases during later developmental stages when a variety of live and dead tree sizes, as well as dead wood on the forest floor, are all present (Spies 1998).

Although these models are useful for conceptualizing structural development in forests subject to stand replacing disturbances, they are typically idealized and based on theory as opposed to empirical data. At a regional scale where multiple vegetation zones occur that vary in current and historical disturbance regimes, climate and topography, and species assemblages, a broader classification system capable of tracking structural development is necessary (O'Hara et al 1996, Hessburg et al. 2000). In forests where multiple, non-linear developmental pathways are possible (Frelich 2002), disturbance has the potential to maintain (Platt et al. 1988) or accelerate structural development (Veblen et al. 1991). A variety of structural conditions in early (Halpern 1988, Donato et al. 2012) and later developmental stages may be possible in a single vegetation zone depending on the environment and disturbance history (McCune and Allen 1985). Likewise, our general concept of age and structural development may be limited at the regional scale by physiological constraints imposed by climate and rates and pathways of structural development. Consequently, a single structural condition may represent multiple successional stages (i.e. old-growth) depending on the vegetation zone in which it is found. As a result there is potential for confusion surrounding specific definitions, especially in issues involving policy and management (Parker et al. 2000, Spies 2004).

Forest structure is a major component of biological diversity (Spies 1998, McComb 2008) and focus of regionally based conservation planning efforts (USDA, DOI, and BLM 1994). As a result, maintaining, creating, and restoring particular elements of forest structure have been much of the impetus behind management pertaining to the conservation of biological diversity in many parts of the world (U.S. Fish and Wildlife Service 2003, U.S. Fish and Wildlife Service 2011). Despite the importance of forest structure as a major component of habitat diversity (McComb et al. 1993, Franklin and Van Pelt 2004, Verschuyl et al. 2008) and application of forest structure types in forest state and transition models and wildlife management guides (Hemstrom et al. 2004, Johnson and O'Neil 2001), there are few empirically based characterizations of stand structure. Developing an understanding of regional scale variation is important for conservation planning and monitoring, as well as for developing advanced theoretical models of forest dynamics that quantifying forest change from a warming climate and altered disturbance regimes.

I used a regional forest inventory representing over 11,000 plots to characterize forest structure on lands of all ownerships across 25 million ha of forested land in the Pacific Northwest to address the following questions:

1) What are the major dimensions of forest structure across a broad geographic extent?
2) Which unique structural conditions are created from different combinations of structural components and how long do they take to develop in different vegetation zones?

3) How does the composition of structural types differ among vegetation zones?

Methods

Study Region

My study region is approximately 25 million ha and includes all forest lands in Oregon, Washington and inland Northern California (Fig. 2.1). The region is highly diverse and includes a variety of vegetation zones due to strong climatic and topographic gradients (Franklin and Dyrness 1973, Barbour and Major 1988, Ohmann and Spies 1998) (Appendix: Fig. A-1.1). The climate is generally mediterranean with most precipitation falling in the winter (though some portions of the eastern part of the region receive a large proportion in summer thunderstorms), but large gradients in precipitation, temperature, and elevation create a wide range of climatic conditions from warm and moist at low elevations near the coast to cold and dry at higher elevation further east.

I acquired a map of the major vegetation zones of the study region (Simpson 2013) from the Ecoshare Interagency Clearinghouse of Ecological Information (www.ecoshare.info/category/gis-data-vegzones) (Fig. 2.1). Ecoshare is an online interagency clearinghouse of ecological data. Each vegetation zone represents a single potential climax vegetation type that would develop in the absence of major disturbance. I stratified the region based on potential vegetation types representing a specific species pool within a defined range of climatic and topographic conditions and historical disturbance regimes (Winthers et al. 2005). Vegetation zones enable the interpretation of structural types in a broader context since the same structural type may represent different developmental stages in different vegetation zones. Major vegetation zones correspond to those presented by Franklin and Dyrness (1973) and can generally be broken into wet and dry forests. Major wet forest vegetation zones are located in the western part of the region and include redwood (*Sequoia sempervirens*)/Sitka spruce (*Picea sitchensis*), Douglas-fir *(Pseudotsuga menziesii*)/tanoak (*Lithocarpus densiflorus*), western hemlock (*Tsuga occidentalis*), Pacific silver fir (*Abies amabilis*), and mountain hemlock (*Tsuga mertensiana*). Major dry forest vegetation zones are located in the eastern part of the region and include western juniper (*Juniperus occidentalis*), ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Psuedostuga menziziii*), grand/white fir (*Abies grandis/concolor*), and subalpine forests dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanii*), and whitebark pine (*Pinus albicaulis*).

Natural and anthropogenic disturbances have influenced the development of forest structure in all vegetation zones. Wildfire played a major role across the entire study region at different time periods (Agee 1993). Historic fire regimes range from high frequency, low severity fire in warm, dry forests to low frequency, high severity fire on cold and wet forests. Much of the vegetation in the region was historically subject to a mixed severity fire regime where the proportion of high severity fire varied spatially and temporally (Agee 1993). Long periods of fire exclusion are believed to have altered forest composition and structure across much of the region, particularly in dry forests of the eastern and southern portions of the region (Perry et al. 2011), but wildfires have increased in frequency and extent since the mid-1950s (Littell et al. 2009). Windstorms and landslides associated with storms off the Pacific Ocean play a far greater role in wet forests than in dry forests, particularly on steep, exposed landforms (Sinton et al. 2000).

In wet forests of the western portion of the study area, widespread clearcut logging in lower elevation private forests began in the late 1800's, but started on federal lands in the 1940s when it reached its peak (Johnson and Swanson 2009). The passage of the Northwest Forest Plan (NWFP) in 1994 essentially stopped clearcutting of older forests on federal lands within the range of the northern spotted owl (*Strix occidentalis caurina*), but clearcutting is still the dominant practices on private forests managed for timber production. Forests in the drier eastern parts of the region were directly affected by grazing of domestic animals and high grade logging with the selective removal of large old-growth ponderosa pine in the early to mid- part of the 20th century (Langston 1995, Hessburg and Agee 2003). Although removal of fine fuels by livestock grazing reduced the role of fire in dry forests during this time, several high severity wildfires affected large areas in the Blue Mountains and Northern Rockies prior to the adoption of a policy of fire exclusion in the 1930's (Langston 1995, Brown 1968). Most vegetation zones have been logged during different periods since the 1900's, but substantial tracts of unlogged forest still remain.

Field Data

I acquired field data on forest structure from 11,091 1 ha plots from the USDA Forest Service Pacific Northwest Research Station Annual Forest Inventory and Analysis program (FIA) PNW-FIA Integrated Database (IDB). Plots were located at a density of approximately one every 2,400 ha across all land ownerships in forested parts of Oregon, Washington, and northern California (Appendix: Fig. A-1.1). Data collection began in 2001 and continued until 2010 and approximately one-tenth of the plots was sampled each year. Plots include a series of four variable radius subplots. Live trees and snags <12.7 cm dbh and of cover of understory vegetation (shrubs, forbs, and graminoids) were measured in 2.1 m radius microplots. Live trees and snags ≥12.7 cm diameter at breast height (dbh) were measured in 7.32 m radius subplots. Live trees and snags ≥76.2 cm dbh on the west side of the Cascade Crest and ≥61 cm dbh on the east side were measured in 18 m radius subplots. Dead and downed wood was sampled along two 7.32 m transects in each subplot.

I acquired plot scale (1 ha) summaries of variables describing live tree structure from the Landscape Ecology, Modeling, Mapping, and Analysis (LEMMA) Project (http://lemma.forestry.oregonstate.edu). These variables included basal area (BA), density (TPH), volume (VOL), biomass (BPH), quadratic mean diameter of all dominant and codominant trees (QMD), basal area-weighted mean dbh of all live trees (DBH), a diameter diversity index (DDI) based on the tree densities in different size classes (Spies and Pabst unpublished), standard deviation of dbh (SDDBH), average height of all dominant and codominant trees (STNDHT), and percent canopy cover of all live trees (CANCOV) as calculated using methods in the Forest Vegetation Simulator (FVS) (Crookston and Stage 1999). This method corrects for overlapping canopies and 100 % canopy closure occurs at about 65% CANCOV. Variables describing dead wood included the density (SPH), and biomass (SBPH) of snags ≥12 cm dbh and ≥2 m tall, as well as the biomass of dead and downed wood ≥12 cm at the large end and ≥3 m long (BDW). The only variable included on understory vegetation was the summed total percent cover of shrubs, forbs, and graminoids (USTORY).

I acquired spatial data on the perimeters of wildfires greater than 400 ha from 1984 to 2010 from the Monitoring Trends in Burn Severity Program (www. mtbs.gov) and overlaid plot locations to classify plots as burned or unburned (Appendix: Fig. A-1.1).

Data Analysis

Question 1: Dimensions of forest structure

I used principal components analysis (PCA) to condense previously listed metrics of stand structure into the major dimensions of forest structure. I chose to use PCA because many structural attributes are linearly related (e.g. live tree biomass and basal area). I used the princomp function in R with the cross-products matrix based on the correlation matrix among variables. Variables included in the PCA were representative of the three components of forest structure including live trees, dead wood, and understory vegetation. All variables were centered to a mean of zero and standardized in order to equalize variance among variables measured in different units.

Question 2: Structural Classification

I performed hierarchical agglomerative clustering with Euclidean distance and Ward's method (Ward 1963) to assign each plot into structure based groups. Agglomerative clustering works by iteratively merging the most similar plots into groups until all groups are merged. I used the hclust.vector algorithm in the package fastcluster in R. The hclust.vector algorithm is equivalent to hclust in the package cluster, but uses less memory and drastically reduced processing time, allowing us to include the full data set in the clustering. Plots were clustered on the axis scores of the first five dimensions of the PCA to reduce redundancy of correlated structural variables (e.g. basal area and biomass) as well as subjectivity or bias in selection of specific variables.

I used data on ages of dominant and co-dominant trees to assign an estimated stand age for each plot. Age of individual trees was estimated in the field from increment cores taken from one live dominant and co-dominant tree for each species. In cases where trees were too large for the increment borer to reach the pith of the tree, age was estimated based on growth in the inner five cm of the core. Stand age was then estimated as the basal area weighted average age of all dominant and co-dominant tree ages in a plot. I compared the plot level median basal area weighted ages of dominant and co-dominants first among structural classes and then among vegetation zones by individual structural classes using notched boxplots. Notched boxplots show the median, interquartile range, and notches that approximate a 95% confidence interval around median values where the lack of overlap between the notches of two boxes provides strong evidence that medians differ (Chambers et al. 1983). I used the median as opposed to mean because the distribution of age values was not always symmetric and to avoid influence from potential outliers.

Question 3: Comparison of the Distribution of Structural Types among Vegetation Zones

I examined differences in forest structure among vegetation zones using two approaches. First, I determined the major gradients in the composition of structural types using Non-Metric Multidimensional Scaling (NMS). NMS is an indirect ordination technique appropriate for detecting compositional gradients in data that are non-normal or on arbitrary scales (McCune and Grace 2002). NMS is frequently used in community studies where plots are used as sample units, which are then sorted along compositional gradients that seek to maintain ranked distances based on compositional similarity. In this analysis, vegetation zones (n=10) were the sample units which were described in terms of the relative abundance of each of the individual structural types. I first used a square root transformation to equalize the relative importance of common and rare structural types, then relativized by vegetation zone total. NMS was performed in PC-ORD 6 (McCune and Mefford 2011) using the slow and thorough settings with Sorenson similarity as a distance measure. This procedure starts with a random starting configuration and 500 runs with real data and steps down in dimensionality starting with six axes using 0.000001 as a stability criterion. Ties were penalized on unequal ordination distance. A Monte Carlo test based on 999 runs was used to test whether NMS was extracting stronger axes than expected by chance. Second, I tested for differences in stand structure at the plot level among vegetation zones using Multiple Response Permutation Procedure (MRPP) using the Vegan package in R. MRPP is a nonparametric multivariate test of the hypothesis of no difference in the mean within group Euclidean distance among vegetation zones (McCune and Grace 2002).

Results

Principal Components Analysis of Structural Variation

The first five PCA axes accounted for 90% of the variance explained (Table 2.1). Axis 1 accounted for 47% of variance and was strongly and negatively correlated with live tree biomass, basal area, DDI, stand height, the standard deviation of dbh, and canopy cover. Axis 2 accounted for 16% of variance and had a strong and positive correlation with the density of trees per ha and strong negative correlation with quadratic mean diameter. Axis 3 accounted for 13% of the variance and had a strong positive correlation with the biomass and density of snags and biomass of dead and downed wood, but a strong negative correlation with density of live trees. Axis 4 accounted for 9% of the variance and had a strong negative correlation with the cover of understory vegetation and the biomass of dead and downed wood. Axis 5 accounted for 6% of the variance and had a strong negative correlation with the volume of dead and downed wood and a strong and positive correlation with the density of snags per ha and the cover of understory vegetation.

Classification of Structural Types

I began interpreting clusters from the classification by iteratively “cutting” the dendrogram (Appendix: Fig. A-1.2) at increasing numbers of clusters representing broad but ecologically interpretable structural groupings with the goal of representing variation along all five PCA axes while still maintaining a manageable number of clusters. The hierarchy of clusters begins with “groups” at the coarsest level which are then broken into “classes”, and then finally into “types”. The initial cut resulted in three clusters representing low (<25 Mg/ha), moderate (25-99 Mg/ha), and high live tree biomass (>100 Mg/ha) structural groups. The second cut resulted in eleven clusters that broke groups into “structural classes” that differ within groups along the second PCA axis representing live tree density and QMD (Fig. 2.2). I continued identifying clusters to include structural variation and arbitrarily stopped at twenty-five clusters which differ along the other axes of variation including snags, understory cover, and biomass of dead and downed wood (Table 2.2, Appendix: Table A-1.1).

The eleven major structural classes are described below based on differences in eight structural variables most strongly associated with the first five PCA axes (Fig. 2.3). I highlight specific types that are noteworthy or archetypal and provide a naming scheme as a quick reference for comparing structural classes and types (Table 2.2). I also provide additional data on the geographic distribution of structural types (Appendix: Fig. A-1.3, Fig. A-1.4, Fig. A-1.5) and the size class distributions of live trees (Appendix: Table A-1.4), snags (Appendix: Table A-1.5), dead and downed wood (Appendix: Table A-1.6), and the proportion of understory cover the breakdown of into shrubs, forbs, graminoids (Appendix: Table A-1.7).

Low Live Biomass Group (<25 Mg/ha) - Structural Class 1 consists of stands with very low live tree biomass, basal area, and density. **Structural Type 1.1** has a very high density and biomass of snags. Over 90% of plots representing this type have burned since 1984. **Structural Type 1.2** is composed of extremely low densities of small trees and has low snag density and biomass. Approximately 38% of plots representing this type have burned since 1984. **Structural Class 2** consists of stands with low biomass and density of live trees. **Structural Type 2.1** has moderate quadratic mean diameter and is composed primarily of medium sized trees with a unimodal live size class distribution. **Structural Class 3** has low live tree biomass but a high density of small trees and represents a single structural type, **Structural Type 3.0**.

Moderate Live Biomass Group (25 - 99 Mg/ha) - Structural Class 4 represents a single structural type, **Structural Type 4.0, and** has low live tree biomass and density with a high quadratic mean diameter and a unimodal live tree size class distribution. **Structural Class 5** has moderate live tree biomass but high density and is generally composed of small and medium trees with low density and biomass of snags and dead and downed wood. **Structural Class 6** has moderate live tree biomass and density but high basal area and quadratic mean diameter and extremely high but variable snag density and biomass and approximately 9% of the plots representing this structural type have been burned since 1984. **Structural Type 6.2** has low live tree biomass and canopy cover with very high quadratic mean diameter and a unimodal live tree size class distribution, but snag density and biomass are extremely high and approximately 70% of the plots representing this structural type have been burned since 1984. **Structural Class 7** has moderate live tree biomass, very high but variable live tree density, and low density and biomass of snags.

High Live Biomass Structural Classes (100 - >300 Mg/ha) - Structural Class 8 has high live tree biomass and density. **Structural Type 8.3** has moderate density with a very high quadratic mean diameter and a high density of big trees with extremely high cover of understory vegetation. **Structural Class 9** has high live tree biomass and very high density while snag density and biomass and the biomass of dead and downed wood are moderate but variable. **Structural Class 10** has very high live tree biomass and high density. Snag density and biomass are high but variable and mean biomass of dead and downed wood is high. **Structural Type 10.3** has extremely high live tree biomass and the highest density of big trees, snag biomass, and biomass of dead and downed wood of this class. **Structural Class 11** has extremely live tree biomass (>300 Mg/ha) and high but variable density. **Structural Type 11.1** has high density as well as high snag biomass and extremely high biomass of dead and downed wood. **Structural Type 11.2** has moderate density with extremely high quadratic mean diameter a unimodal live tree size class distribution with very high understory cover.

Age Differences among Structural Classes

Patterns of median age across structural classes varied among vegetation zones (Figs. 2.4 and 2.5). Stand age generally increased with live biomass in wet vegetation zones, but showed little relationship to biomass in dry vegetation zones, with the exception of Douglas-fir and grand fir/white fir where median age was greatest in the highest biomass classes. Median age of dominant and co-dominant trees frequently differed among vegetation zones for individual structural classes (Appendix: Fig. A-1.6, Fig. A-1.7, Fig. A-1.8). The major exception to this is in dry vegetation zones and in Structural Class 1 where the median age was zero and there was no evidence of differences among vegetation zones. Median age of structural classes was generally lowest in western hemlock and Sitka spruce vegetation zones and highest in mountain hemlock and western juniper zones.

Distribution of Structural Classes and Types by Vegetation Zone

Regional Distribution of Structural Classes

The relative abundance of individual structural classes differed by as much as five times across the full study region and ranged from a low of 2.5% for Class 1 to a high of

14.8% and 14.2% for classes 7 and 9, respectively (Fig. 2.6, Appendix: Table A-1.2). Low live biomass classes (1-3) make up 14.7 % of the forested area. These are mostly composed of Class 2 (Low Live Biomass and Density) and Class 3 (Low Live Biomass and High Density), both of which account for at least 2% of all forests. Class 1 (Very Low Live Biomass and Density) is the rarest of all structural classes (<2% of all plots). Moderate live biomass structural classes (4-7) make up 41% of the forested area and mostly composed of Classes 5 and 7. Type 6.2 (Moderate Live Biomass w/ Big Trees & Very High Snag Density and Biomass) is regionally rare (<1%). High live biomass classes make up 44% of the forested land area with each individual class comprising at least 12 % of the area with the exception of Class 11 (Extremely High Live Biomass w/ Giant Trees) which occurred in only 5.5% of the study extent.

Distribution of Structural Types by Vegetation Zone

The NMS of vegetation zones by structural types resulted in a two dimensional solution accounting for 98.7 % of the variance (final stress=2.5, instability=0.00000). Axis 1 accounted for nearly all the variance explained (94.1%) and represents a gradient dominated by high basal area and density structural classes in Douglas-fir, tanoak, Pacific silver fir, and mountain hemlock vegetation zones to lower density and basal area structural classes in western juniper and ponderosa pine (Fig. 2.7). Axis 1 had strong positive correlations with abundance of Structural Types 5.3, 7.2, 7.3, 9.2, 9.3, and 10.2 as well as strong negative correlations with amount of Structural Types 2.1, 2.2, 4.0, 5.1, and 5.2 (Table 2.3). Axis 2 accounted for only 4.6% of variance explained and represents a gradient from increasing abundance of structural types with high snag density from subalpine vegetation zone to the western hemlock and Sitka spruce-redwood vegetation zones with lower snag density types (Fig. 2.7). Axis 2 had very strong positive correlations with high biomass Structural Types 8.3 and 11.2 as well as very strong negative correlations with low biomass Structural Types 1.1 and 6.2. The composition of structural types differed significantly among vegetation zones (MRPP, p=0.001, A= 0.09).

Discussion

Major Dimensions of Forest Structure

Most variation in forest structure across the Pacific Northwest can be broken down along a few major axes of variation related to live tree biomass, density and size of live trees, and snag abundance. Variables related to live tree biomass accounted for most of the variance, but were strongly related only to a single principal component, whereas other variables were related to multiple components. Although some structural variables related to each other in ways predicted by current theory on succession and stand dynamics (e.g. live biomass and density), there was less correspondence between some variables (e.g. canopy cover and cover of understory vegetation) than expected. These results demonstrate that some attributes of forest structure often act independently or relate to other attributes in multiple ways, and that structural development is not always associated with a monotonic accumulation of live tree biomass.

The dominant gradient in forest structure was most strongly related to live tree biomass, basal area, and the presence of big trees (DDI and QMD). Although past regional scale work shows that the potential accumulation of live and dead biomass with age is constrained by mainly by climatic factors such as temperature and moisture that drive productivity (Gholz 1982, Malhi et al. 2006, Hudiburg et al. 2009). However, large diameter trees (e.g. > 100 cm) can also be found in dry forests where quadratic mean diameter may be very high, but where trees are shorter and occur at much lower densities, thus limiting the accumulation of total live biomass. The low end of the live biomass dimension may also be related to productivity where structural development is slow in hot, dry or cold environments, but low biomass conditions can also occur in high productivity environments as a result of natural disturbance and timber harvesting (Ohmann et al. 2007, Urquiza-Haas et al. 2007, Hudiberg et al. 2009).

Density and quadratic mean diameter both had strong, but inverse, correlations with the second major gradient in structure which ranges from high density forests with small trees to lower density woodlands with bigger trees. Along with live tree density, snag density was also positively correlated with Axis 2 indicating an upper boundary of density with the accumulation of live tree biomass similar to the "self-thinning line" (Reineke 1933, Yoda et al. 1963). My results indicate that maximum density occurs at intermediate levels of live biomass after which self-thinning related mortality begins. Past studies in the Pacific Northwest show that this upper boundary varies among species and with site productivity (Weiskittel et al. 2009, Zhang et al. 2013) and climate (Monserud et al. 1990, Weiskittel et al. 2011), but results of this study show that even most dry vegetation zones are well represented towards the high live tree density/low QMD end of the second PCA axis. High density in dry forests is most likely the result of densification of woodlands associated with fire exclusion and other anthropogenic changes to historical disturbance regimes over the 20th century (Hessburg and Agee 2003, Youngblood et al. 2004, Merschel et al. 2014).

The third dominant dimension in forest structure was most strongly related to snag density and biomass as well as biomass of dead and downed wood and represents a variation in levels of recent tree mortality with more open canopy and lower density of live trees indicative of post high severity disturbance. Although epidemic outbreaks of insects and pathogens and disease have the potential to result in high levels of tree mortality (Raffa et al. 2008), most of the variation on the high end of Axis 3 is the result of recent wildfires. Wildfires have increased in extent in the region since the mid-1950's (Littell et al. 2009), but little is known regarding the cumulative effects of recent wildfires on structural variation at larger scales. These results indicate that wildfires have increased structural variation across the region, adding an important dimension of structure generally not present in unburned forests. Many of the plots with high amounts of dead wood also have low live tree biomass indicative of stand replacing wildfire, but these make up a small proportion of plots, and most forests in the region have few snags in relation to the density of live trees. In addition, burned plots at the high end of Axis 3 occur across the full range of the live tree biomass dimension (Axis 1) in burned forests, suggesting that much of the wildfire was either moderate in severity resulting in partial stand replacement, or low severity with mortality rates within the range of that found in unburned forests.

Although the fourth PCA axis accounted for less variance than the first three axes, the strength of its correlation with understory vegetation underscores its importance as a dimension of forest structure. Traditional models of stand development suggest that understory cover and diversity are lowest during canopy closure and stem exclusion phases due to the level of canopy dominance exerted by trees (Oliver and Larson 1990, Franklin et al. 2002). My results showed only weak correspondence between understory cover and attributes of live tree structure such as density, canopy cover, and basal area, indicating that understory vegetation often acts independently of overstory structure. Other recent studies in temperate and boreal forests have found similar results with overstory trees exerting weak control over understory dynamics following clearcut logging and wildfire (Hart and Chen 2008, Halpern and Lutz 2013). Instead, life history characteristics of both pre- and post-disturbance vegetation (e.g. shade tolerance, reproductive mode) are important influences on temporal changes in cover of understory vegetation (Burton et al. 2013). In many forests, understory vegetation may actually exert control on forest structure through competitive interactions with tree regeneration (Riginos 2009) and by providing fuel to carry low intensity surface fire (Noss 1989, Heyerdahl et al. 2014).

The final PCA axis represented the abundance of dead and downed wood. This dimension is constrained by input directly from live trees or snag fall as well as by losses through decomposition (Harmon et al. 1986). Mortality of individual large trees in old-growth forests can be a slow but persistent input of downed dead wood that can lead to high levels of dead wood if rates of decomposition are relatively slow (Harmon and Hua 1991). Pulses of large amounts of dead and downed wood can also result from infrequent, intense disturbances making it an important component of early seral forest structure as well. As a result, the distribution of dead and downed wood biomass along a chronosequence of age is U-shaped (Spies et al. 1988). However, in uneven-aged forests where disturbances are non-stand replacing the relationship may differ smaller scale disturbances result in occasional pulses of dead wood (Fraver et al. 2002). The rarity of forests with extremely high biomass of dead and downed wood may explain the relatively low amount of variance explained by Axis 5, while the strength of its correlation is indicative of the unique structural conditions created by large amounts of dead and downed wood. As a result, biomass of dead and downed wood emerged along multiple axes first with snags along Axis 3, and then with understory vegetation along Axis 4.

Regional Structural Classification

I further characterized structural types into developmental stages to improve ecological interpretation of potential disturbance histories (Table 2.4) and correspondence with existing models of structural development. A given structural type may be the result of a variety of disturbance histories and represent multiple developmental stages depending on vegetation zone. Patterns in ecological systems are often the result of multiple processes, and any prediction regarding pattern must be derived not only from the patterns themselves, but from an understanding of the variety of processes that might be operating to create them (Cale et al. 1989).

Low Live Biomass Structural Group

Some structural types in the low live biomass group correspond well with stages in age/process-based classifications of stand development following stand replacing disturbance (Bormann and Likens 1979, Oliver and Larson 1990, Franklin et al. 2002) and are generally representative of early successional forests. Although there is no widely accepted single definition, low biomass structural types share a variety of commonalities including low canopy cover, live tree density, and basal area which are generally cited as major characteristics of early seral habitats (Swanson et al. 2011). Despite these similarities, age varies widely among vegetation zones, and low biomass structural types demonstrate the variation in early developmental stages depending on the nature and severity of recent disturbance as well as rate of establishment and regrowth.

Structural types in Class 1 (Extremely Low Biomass) represent post-stand-replacement disturbance and legacy creation prior to the establishment of trees (Franklin et al. 2002). Differences in the abundance of snags and dead and downed wood in the types that make up this class highlight the contrast in post-stand replacing disturbance structural conditions depending on the nature and severity of the disturbance that creates them. The high amount of variation in snag density and biomass in Type 1.1 (Extremely Low Live Biomass w/ Snags) demonstrates the potential structural diversity during early developmental stages, particularly following wildfire. These results substantiate the need to differentiate among early developmental stages which may vary in function as dead biological legacies have the potential to increase structural complexity in early developmental stages (Donato et al. 2012) and provide important habitat elements for a variety of organisms (Hutto 2008, Swanson et al. 2014 *In press*).

Structural types in Class 2 (Low Live Biomass and Density) include early developmental stages where trees have established but the canopy is still open and there is very little dead wood. Higher live tree density and J-shaped size class distributions in

Type 2.2 (Low Live Biomass & Density w/ Small Trees) suggest continuous recruitment at high density similar to the cohort establishment phase (Franklin et al. 2002), stand initiation (Oliver and Larson 1990), and/or reorganization phase (Bormann and Likens 1979). However, the unimodal live tree size class distribution in Type 2.1 (Low Live Biomass & Density w/ Medium Trees) indicates an alternative stage where protracted recruitment may be episodic with individual establishment occurring in pulses spaced between periods of no establishment. Although forests in this class could be regenerating clearcuts with full biomass removal, lack of snags and dead and downed wood suggest that many are either aggrading forests in shrublands, grasslands, or meadows. These types are most abundant in dry forests where protracted establishment may be associated with competition from shrubs or herbaceous vegetation (Riginos 2009) or exogenous processes related to climatic fluctuations (Brown et al. 2005), dispersal limitation (Agee and Smith 1984), or a combination of these factors (Acacio et al. 2007).

Structural Class 3 is composed of densely regenerated stands approaching canopy closure, similar to the end of the stand initiation (Oliver and Larson 1990) and beginning of canopy closure (Franklin et al. 2002) phases. High variation in biomass of dead and downed wood may be related to fire history, the number of times the site was logged, and management practices regarding the residual dead wood management practices (Spies and Cline 1988). Although the scale and frequency of disturbance affects the extent of early successional habitats (Lorimer and White 2003), differences in median ages of Class 3 among vegetation zones demonstrates that rates of post stand-replacement recovery reflect a regional gradient in productivity and will thus affect the persistence of this developmental stage (Yang et al. 2005).

Moderate Live Biomass Structural Group

Some structural classes and types in the moderate live biomass group also correspond with current models of stand development, but several types with lower density and bigger trees represent alternative stages that lack analogs in existing structural classifications. Structural classes and types in the moderate live biomass group represent a wide array of mid, late, and even early successional forest stages based on differences in age among vegetation zones.

Structural Classes 5 (Moderate Live Biomass and High Density) and 7 (Moderate Live Biomass and Very High Density) are similar to developmental stages such as aggradation (Bormann and Likens 1979), stem exclusion (Oliver and Larson 1990), and biomass accumulation/competitive exclusion (Franklin et al. 2002). Abundance of snags and dead and downed wood is generally low, and these forests are less structurally complex than those that were naturally regenerated after wildfire (Spies et al. 1988). These classes date back to the mid and late 20th century in wet forests indicating that most likely established following widespread clearcut logging on public and private lands (Johnson and Swanson 2009). Denser types in Class 7 have similar density and basal area as second growth forests established following clearcutting in western hemlock forests (Lutz and Halpern 2006), but lower density types in Class 5, particularly Type 5.2, are similar in structure to recently thinned stands in western hemlock forests (Chan et al. 2006, Davis et al. 2007). These classes are older in dry forest where they date back to the early part of the 20th century when high severity fires associated with high fuel loads from logging slash where common (Pyne 1982) and high-grade logging was most the most common harvesting practice (Hessburg and Agee 2003). Structural types in Class 5 have similar basal area and density to plantations and stands that may or may not have been thinned, while types in Class 7 are more likely naturally regenerated after fire or logging with little subsequent management (Cochran and Barrett 1993, Cochran and Barrett 1998, Cochran and Barrett 1999, Harrod et al. 1999). In very dry and higher elevation vegetation zones where productivity is low, logging was far less prevalent, and fire return intervals were longer, these structural classes may represent old woodlands that have been increasing in density for over a century (Waichler et al. 2001), but some also date back to a period of widespread fire during the 19th century (Weisberg and Swanson 2003).

Structural Classes 4 (Moderate Live Biomass and Low Density w/ Big Trees) and 6 (Moderate Live Biomass & Low Density w/ Very High Snag Density) lack analogs in current models of stand development. These represent woodlands with big trees but a range of live tree densities and an abundance of snags and dead and downed wood. Structural Class 4 is a later developmental stage in lower productivity vegetation zones where most stands pre-date the 20th century. It is likely the result of protracted establishment associated with climatic or topographically related water limitation given its geographic distribution very dry forests. However, structure is also very similar to stands that have been recently thinned for restoration and reduction of risk of high severity fire in dry forests including grand fir/white fir and Douglas-fir (Harrod et al.

2009). In more productive vegetation zone forests, this structural class may occur where local topo-edaphic and soil conditions cause relatively xeric conditions, or where silvicultural treatments such as variable-retention harvests have taken place recently (Acker et al. 1998, Maguire et al. 2007). Structural Class 6 represents a developmental stage where forests are thinning from high levels of mortality potentially associated with pathogens, insects and wildfire which are primarily killing smaller trees and increasing quadratic mean diameter. Partial stand replacing wildfires are primarily responsible for maintaining Type 6.2 (Moderate Live Biomass and Density w/ Big Trees and Extremely High Snag Density and Biomass), although epidemic insect, pathogen and disease outbreaks could also play a role. This types is unique and highly structurally diverse with have elements late successional types (e.g. big, old remnant trees, big snags, abundant dead wood). I classify this as an early developmental stage based on high snag density and low canopy cover.

High Live Biomass Structural Group

Structural classes in the high live biomass group generally represented later developmental stages as described in previous models of stand development with high densities of big trees and the occurrence of bigger snags and the accumulation of dead and downed wood. Structural classes in this group also represent the diversity of later developmental structural stages across the region.

Classes 8 and 9 are similar to the end of biomass accumulation and stem exclusion phases and beginning of the maturation (Franklin et al. 2002), understory re-initiation (Oliver and Larson 1990), and transition phases (Bormann and Likens 1979).

Stand ages in both of these classes in wet forests correspond with a period of widespread logging in the early to middle part of the 20th century, but the abundance of dead and downed wood in larger size classes in some types (Type 8.2, 9.3) suggests that these may also have established after stand replacing fire. Basal area and density in Class 8 are similar to current plantations (Davis et al. 2007) or naturally regenerated stands that have been thinned in the past few decades (Bailey and Tappeiner 1998a), whereas density in Class 9 is similar to naturally regenerated stands that have received little management (Bailey and Tappenier 1998, Raymond and Peterson 2005). Structural types in Classes 8 and 9 are late successional in dry forests because most predate early 20th century high grade logging and stand replacing wildfire and have high densities of big trees that correspond with historical reconstructions (Harrod et al. 1999, Hagmann et al. 2013, Merschel et al. 2014). However, overall density and basal area are much higher than historic conditions in some dry forests where fires have been excluded during the 20th century (Youngblood et al. 2004).

Structural Classes 10 and 11 represent what have traditionally been called late successional and old-growth forests (Oliver and Larson 1990, Spies and Franklin 1991) and have the oldest dominant trees and highest levels of live and dead biomass (D'Amato et al. 2008, Burrascano et al. 2013). Variation in age for plots in these classes among vegetation zones demonstrates that rates of development of older forest structural characteristics vary with productivity (Larson et al. 2010). High densities of big trees and abundant dead and downed wood indicate that Class 10 represents late successional forest, but it also represents old-growth in some dry or cold lower productivity vegetation zones. Class 10.3 is similar to the transitional phase (Bormann and Likens 1979) or maturation phase (Franklin et al. 2002) where mortality of large trees in the initial cohort results in big snags and an accumulation of dead and downed wood in the larger size classes. Structural Class 11 represents old-growth in wet forests with the maximum accumulation of live and dead biomass after centuries of growth with high densities of big trees and dead biomass in large snags and pieces of dead and downed wood. These classes are found mostly in productive wet forests and are rare in dry forest with the exception of some in the most productive vegetation zones including grand/white fir and Douglas-fir. Stand ages are typically the oldest in these classes depending on vegetation zones. In addition, the wide range of mean age indicates they have the potential persist for centuries.

Distribution of Structural Types by Vegetation Zone

Structural variation and diversity of structural types in forests of the Pacific Northwest correspond with major gradients in climate and productivity as well as differences in historical and contemporary disturbance regimes. Most forests across the region have moderate to high levels of biomass and are in mid developmental stages or beginning to mature towards later developmental conditions, but this differs substantially by vegetation zone. Low biomass early successional forests and extremely high biomass late successional forest are less common, but their abundance varies widely by vegetation zone. Wet forests are dominated by forests in mature and late developmental stages, whereas dry forests have a greater range in the composition of structural types with more low and moderate biomass types that represent multiple developmental stages.

Wet Forests

Low biomass structural types are by far the least abundant in wet forests and are primarily comprised of Type 3, most of which resulted from timber harvest which has been the most common stand replacement disturbance in wet forests since the early 1970's (Healey et al. 2008). Low biomass types representing diverse early successional forests with live and dead biological legacies (e.g. Types 1.1 and 6.2) are exceedingly rare, except where individual large wildfires have burned in Douglas-fir/tanoak (Biscuit 2002) and mountain hemlock (Charlton 1996, B&B 2003) forests near wet/dry forest boundaries. Declines in early successional forests have been observed around the world (Angelstam 1998, Trani et al. 2001) and linked with corresponding losses in biodiversity (Pimm and Askins 1995, Betts et al. 2010), and creation of diverse early successional forests in wet forests has been a focus of some recent forest management proposals in the Pacific Northwest (Franklin and Johnson 2012). My results provide information on the diversity, extent, and persistence of early successional forests in the Pacific Northwest and support the hypothesis they are currently rare in wet forests.

Moderate biomass structural types make up about twice as much of wet forests as low biomass types and are mostly comprised of higher density types, particularly those in Class 7. These forests date back to the mid and late 20th century when clearcutting was followed by replanting at high densities (Curtis et al. 1998), and the establishment of plantations was widespread, particularly in the western hemlock zone (Johnson and Swanson 2009). These plantations currently provide the major source of timber on federal lands where policy shifts during the 1990's caused harvesting practices to shift from clearcutting of late successional and old-growth forests to thinning of forests less than 80 years old. The abundance of Class 5 suggests that some recent mechanical thinning has occurred, but is limited in relation to the amount of Class 7. Likewise, while variable retention harvests have been increasingly common on federal lands since the mid-1990's (Aubry et al. 2009), the low abundance of Type 4 suggests that their application is still low in proportion to the amount of Class 7. In less productive, higher elevation mountain hemlock and silver fir vegetation zones where clearcutting was less prevalent, moderate biomass structural types are probably the result of aggrading meadows or stand-replacing wildfire which was widespread in the 19th century (Weisberg and Swanson 2003) and are now maturing. The relatively low abundance of forest in Class 6 suggests that recent episodes of mortality in wet forests have been rare with the exception of mountain hemlock where it is almost twice as abundant as in other vegetation zones. Although the occurrence of Type 6.2 is related to wildfire, 6.1 is more likely associated with laminated root rot (*Phellinus weirii*) which can cause small localized patches of mortality in mature mountain hemlock trees (Hansen and Goheen 2000).

Wet forests are predominantly composed of high biomass structural types. Most of the high biomass structural types in the Sitka spruce-redwood and western hemlock vegetation zones are mature plantations that developed rapidly following timber harvest in the early 20th century, but some apparently regenerated following stand-replacing wildfires around the same time (e.g. Types 8.2, 9.3). These are less common, but can be locally abundant as with Type 8.2 which is particularly abundant around the vicinity of

Tillamook, Oregon where a series of high severity wildfires occurred in the 1930's and 1940's (Lucia 1983). Thinning to accelerate late successional conditions in future forests has potentially increased the abundance of Type 8.3 with lower density and a greater cover of understory vegetation (Bailey et. al 1998b). A combination of high severity 19th century wildfire and extensive clearcutting in the 20th century decreased the abundance of late successional very high and extremely high biomass structural types in western hemlock and Sitka-spruce/redwood vegetation zones (Spies and Duncan 2009), but late successional forests are far more abundant in the higher elevation silver fir and mountain hemlock vegetation zones where cutting was less prevalent.

Dry Forests

The relative abundance of early developmental low biomass structural types varies in dry forests but increases in the drier, lower elevation vegetation zones. The prevalence of low biomass structural types in the western juniper and ponderosa pine vegetation zones is probably related to climate and site productivity. Tree establishment in shrublands and grasslands during the 20th century has increased the extent of structural Type 2.1 in western juniper (Miller and Rose 1995) and even ponderosa pine which has been invading non-forested areas in other parts of the western United States (Mast et al. 1997). Declines in timber harvest beginning in the 1980s (Adams and Latta 2007) have limited the extent of structural early developmental structural types associated with clearcutting (e.g. Types 3 and 1.2), but recent wildfires are responsible for presence of other early successional low biomass types in dry forests. Type 1.1 is most abundant in subalpine forests where recent fires have been relatively common, but these early seral forest conditions represent a small proportion of the total forested area indicating that despite increases in wildfire in the region, this type is still one of the rarest in the region. Fires are thus providing important wildlife habitat for some species (Hutto 2006) and potentially increasing structural diversity at the regional scale. However, my results show that the amount of stand-replacing fire varies tremendously with scale and geographical location and is located in a few “hotspots” associated with very large wildfires in the Klamath (Biscuit 2002), Eastern Cascades/Cascades (B&B 2003), and North Cascades (Tripod 2007) ecoregions and thus may be reducing structural diversity at smaller landscape scales.

Structural types in the moderate biomass group are generally the most abundant in dry forests where they represent a variety of mid, mature, and late developmental stages. Structural types in Classes 4 and 5 are the most common moderate biomass forests in western juniper where they are woodlands in mature and late developmental stages. These were historically restricted to sites offering refuge from fire, but have been encroaching on sagebrush steppe over the last few centuries (Miller and Rose 1999), altering hydrology and reducing habitat for sage-grouse (*Centrocercus urophasianus*) (Miller et al. 2005). Class 4 resembles historical woodlands in xeric ponderosa pine forests where it is still common, but has a much lower density of big trees than historically (Youngblood et al. 2004). In other dry forests, Class 4 is likely the result of recent thinning (Harrod et al. 2009) or aggrading forests that have invaded meadows and shrub lands throughout the 20th century in more productive grand/white fir (Halpern et al. 2010) and subalpine forests (Zald et al. 2012). The higher abundance of the dense moderate biomass structural types in Classes 5, 6, and 7 in dry forests is a reflection of the legacy of fire suppression, grazing, and past forest management practices during the 20th century aimed at converting mixed age forests to even aged stands (Johnson et al. 1994). Forests represented by Class 5 are most abundant in the lower, more accessible ponderosa pine vegetation zone where repeated high grading removed all large trees and recent mechanical thinning or old treatments with prescribed fire to reduce fire risk have been common (Peterson et al. 2005). The denser structural types in Class 7 are more abundant than Class 5 in the more remote and productive, higher elevation grand fir and Douglas-fir vegetation zones as a result of fewer logging entries and a greater growth response to high grading and fire exclusion (Merschel et al. 2014). Structural types in Class 7 do have remnant old trees, but current structure is departed from historical conditions and they currently have higher overall tree density (Baker 2012) but lower density of big trees (Harrod et al. 1999, Hagmann et al. 2013, Merschel et al. 2014). Recent legislation (SB 5521 Oregon Federal Forest Health Package) is focused on restoring structure in these forests by reducing density and ideally increasing resilience to future drought and wildfire. The abundance of Class 6 suggests that recent episodes of mortality associated with insects and disease as well as increasing extent of wildfire have already begun affecting some remnant late successional forests. However, these disturbances appear to be creating a more open woodland structure by lowering live tree density and increasing the dominance of bigger trees in Type 6.1. Wildfires are also increasing the abundance of the structurally diverse Type 6.2 with big remnant trees which is generally very rare.

The abundance of structural types in the high biomass classes varies widely in dry forests where they represent late successional forests and are generally restricted to more productive, higher elevation dry forests. Late successional high biomass structural types are common in subalpine forests where there has been little wildfire or logging during the 20th century logging. Likewise, high densities of big trees in high live biomass forests in white fir/grand fir and Douglas-fir vegetation zones may also have escaped much of the high grade logging in the early 20th century. However, rapid growth of trees in these vegetation zones suggests that some big trees may be relatively young (Merschel et al. 2014), thus although the big tree component of structure may be similar, composition of these forests may be departed from historical conditions. Either way, the effects of fire exclusion are apparent in that the current density of all trees is still much higher compared with historical data (Baker 2012, Hagmann et al. 2013) and reconstructions (Harrod et al. 1999, Ohlsen and Schellhaas 1999, Merschel et al. 2014). High biomass forests with low density (8.3) that were a major component of ponderosa pine and grand/white fir, and Douglas-fir vegetation zones (Agee 2003, Hagmann et al. 2013) are very rare in white fir/grand fir and Douglas-fir vegetation zones and were undetected in ponderosa pine. Extremely high biomass structural types are very rare and limited to white fir/grand fir and Douglas-fir where they persist in topographically related fire refugia or other remote areas that were not logged (Camp et al. 1997).

Conclusion

This study provides the first empirically-based regional-scale characterization of the major components and patterns of forest structure and how they vary in relation to age, vegetation zone, and disturbance history. Although most of variation in forest structure was accounted for by live tree biomass, other components including tree size and density, dead wood, and understory vegetation cumulatively accounted for as much variation. Although some structural components related to each other in ways predicted by current theory on structural development (e.g. live biomass and density), there was less correspondence between some variables (e.g. canopy cover and cover of understory vegetation) than previously assumed in existing models of structural development. My results indicate that structural development across regional gradients in environment, species composition, and disturbance history is more complex than the monotonic accumulation of live biomass often depicted in simple conceptual models of stand development and that some components of structure may act independently or emerge at multiple points during development.

The classification of structural types at the scale of a region reveals the diversity of ways interactions among individual components may be expressed in stand-scale structural conditions. A structure based approach offers a viable option for conceptualizing structural development, but ecological interpretation of structural patterns requires an explicit understanding of both environment and historical land use legacies and can benefit greatly through the integration of age and process based understanding. Low biomass structural types represent the first overall characterization of early developmental stages. These can serve as a reference and starting point for assessing the contribution of pre-canopy closure forests to landscape diversity and for developing strategies aimed at conserving them. Moderate live biomass structural types represent a variety of mid, mature, and late successional forests and are the result of multiple developmental histories. Moderate live biomass types with lower density and bigger trees have received little attention in forest planning and conceptual models of structural development, but are potentially going through some of the most rapid structural change associated with mortality. Finally, structural classes in the high live biomass group demonstrate the diversity of mature and late developmental stages across environments and vegetation zones in a region that supports millions of hectares of old-growth forest.

The range of structural variation and diversity of structural types in forests of the Pacific Northwest are related to broad gradients in climate and productivity and differences in historical and contemporary disturbance regimes. Although age typically increased with basal area across structural types in wet forests, the relationship between age and structural class was much weaker in dry forests where the concept a history of mixed severity fire regimes and pathogen outbreaks have created a complex mosaic of forest structure and wide range of tree ages on a site. Most forests in wet vegetation zones had moderate to high levels of live biomass, but were primarily mid and mature developmental stages with low structural complexity that developed following 20th century clearcutting. Late successional structural types, which have been the target of 20th century logging and the focus of considerable conservation efforts within the region (Spies and Duncan 2010), were still relatively common in the wetter vegetation zones, especially those at higher elevation. The abundance of late successional forest in the Northwest Forest Plan area has decreased since the mid-1990s (~6 %) as a result of losses mostly due to wildfire on federal land and logging on private land, but future losses may eventually be offset by gradual recruitment of mature forests which are abundant (Davis et al. 2014 *In press*). On the contrary, diverse early successional forests, which are now the subject of heightened conservation concern (Swanson et al. 2010, Swanson et al. 2014) were exceedingly rare, and most forests in early developmental stages lacked dead wood and were the result of timber harvest. Dry forests had a much greater range of variation in structural types than wet forests. The relative abundance of low biomass structural types increased in higher elevation vegetation zones where the abundance of diverse early successional forests was greatest as a result of recent wildfires. This analysis supports the hypothesis that many dry forests (ponderosa pine, grand fir/white fir, and Douglas-fir) currently exist in a structural state characterized by high density and moderate to high levels of biomass, presumably as a result of fire suppression and past logging practices. On the contrary, low density forests with high density of large trees that would have been a major component of these vegetation zones (Agee 2003) are relatively rare.

The empirical analysis provides a flexible and relatively simple framework for conceptualizing and understanding regional forest dynamics and reveals relationships among structural components, structural conditions, and patterns that both support and challenge existing conceptual models of structural development. Although this study is just a snapshot of structural conditions during the first decade of the 21st century, it reveals the wide diversity of structural types and potential complexity from various combinations of the major components of forest structure. It provides a reference against which to evaluate historical and potential future forest changes in landscape diversity associated with both early and late seral forest and other less well understood stages that result from the interaction of environment, vegetation, and disturbance.

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Table and Figures

Table 2.1. Axis scores for the first five dimensions of a Principal Components Analysis on the following attributes of forest structure: BA=basal area, TPH=density of live trees, BPH=live tree biomass, QMD=quadratic mean diameter, DDI= diameter diversity index, SDDBH=standard deviation of diameter at breast height, STNDHGT=stand height, CANCOV=canopy cover, STPH=snag density, SBPH=snag biomass, DBPH=biomass of dead and downed wood, USTORY=cover of understory vegetation.

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Proportion of Variance (total=0.90)	0.47	0.16	0.13	0.09	0.06
BA	-0.39	.	.	.	.
TPH	.	0.60	-0.33		
BPH	-0.4	.	.	.	.
QMD	-0.25	-0.53	.	.	.
DDI	-0.38	.	.	.	.
SDDBH	-0.34	-0.27	.	.	.
STNDHGT	-0.35	-0.24	.	.	.
CANCOV	-0.33	0.29	-0.3	.	.
STPH	.	0.24	0.56	.	0.42
SBPH	-0.23	.	0.58	.	.
DBPH	.	.	0.32	-0.34	-0.81
USTORY	.	.	.	-0.92	0.35

Table 2.2. Ordinal classification levels of eight structural variables most highly correlated with the first five PCA axes by structural class and type based on the following: Live Biomass (Mg/ha): Very Low=0-4.9, Low=5-24.9, Moderate=25-99.9, High=100-199, Very High=200-299, Extremely High=>300; Basal Area (m^2/ha): Very Low=<5, Low=5-9.9, Moderate=10-19.9, High=20-39.9, Very High=40-59.9, Extremely High=>60; Quadratic Mean Diameter (cm): Very Low (<10), Low (10-19.9), Moderate (20-29.9), High (30-39.9 cm), Very High (40-49.9 cm), Extremely High (>50 cm); Density (trees/ha): Very Low (<100), Low (100-249), Moderate (250-499), High (500-999), Very High (1000-2499), Extremely High (>2500); Snag Density (snags/ha): Very Low (>10), Low (10-24.9), Moderate (25-49), High (50-99), Very High (100-199), Extremely High (>200); Snag Biomass (Mg/ha): Very Low (<5), Low (5-9.9), Moderate (10-24.9), High (25-49.9), Very High (50-74.9), Extremely High (>75); Biomass of Dead and Downed Wood (Mg/ha): Very Low (<5), Low (5-9.9), Moderate (10-24.9), High (25-49.9), Very High (50-74.9), Extremely High (>75); Understory Cover (%): Very Low (<5), Low (5-24.9), Moderate (25-49.9), High (50-74.9), Very High (75-89.9), Extremely High (>90).

Group	Structural Class and Type	Class Type	Live Tree Biomass	Basal Area	Quadratic Mean Diameter	Density	Snag Density	Snag Biomass	Biomass of Dead & Downed Wood	Understory Cover
Low Live Biomass	Very Low Live Biomass & Density	1	VL	VL	VL	VL	VH	M	M	M
	w/ Very High Snag Density & Biomass	1.1	VL	VL	VL	VL	XH	VH	M	M
	w/out Snags	1.2	VL	VL	VL	VL	L	VL	M	M
	Low Live Biomass & Low Density	2	L	VL	M	L	VL	VL	VL	M
	w/ Medium Trees	2.1	L	L	M	L	VL	VL	VL	M
	w/ Small Trees	2.2	VL	VL	L	L	L	VL	L	H
	Low Live Biomass & High Density w/ Small Trees	3 3.0	L	L	L	H	L	VL	H	VH
Moderate Live Biomass	Moderate Live Biomass & Low Density w/ Big Trees	4 4.0	M	M	H	L	VL	VL	L	H
	Moderate Live Biomass & High Density	5	M	M	L	H	L	VL	L	L
	Very High Density w/ Medium Trees	5.1	M	M	L	VH	VL	VL	L	M
	Moderate Density w/ Medium Trees	5.2	M	M	M	M	L	VL	L	L
	w/Big Trees & No Understory	5.3	M	H	M	H	M	L	M	VL
	Moderate Live Biomass & Density w/ Big Trees & Very High Snag Density	6	M	H	H	M	VH	M	M	M
	& High Snag Density	6.1	M	H	H	M	H	M	M	M
	& Extremely High Snag Density & Biomass	6.2	M	M	VH	M	XH	XH	H	M
	Moderate Live Biomass & Very High Density	7	M	H	L	VH	L	VL	M	H
	& High Density	7.1	M	H	M	H	L	VL	L	H
	& Very High Density	7.2	M	H	L	VH	M	VL	M	H
	& Extremely High Density	7.3	M	H	M	XH	L	VL	M	H
High Live Biomass	High Live Biomass & Density w/ Big Trees	8	H	H	H	H	M	L	H	VH
	& Low Dead Biomass	8.1	H	H	M	H	L	VL	M	VH
	& Very High Biomass of Dead & Downed Wood	8.2	H	H	M	H	M	L	VH	H
	& Moderate Density w/ Big Trees	8.3	VH	VH	VH	M	M	L	M	XH
	High Live Biomass & Very High Density w/ Big Trees	9	H	VH	M	VH	H	M	M	M
	& Moderate Dead Biomass	9.1	M	H	L	VH	H	M	M	H
	& Low Dead Biomass	9.2	H	VH	M	VH	M	L	M	M
	Extremely High Density w/ Big Trees & High Dead Biomass	9.3	H	VH	L	XH	VH	H	H	M
	Very High Live Biomass & High Density w/ Large Trees	10	VH	VH	H	H	VH	H	H	M
	& High Dead Biomass & Understory Cover	10.1	VH	VH	H	H	VH	H	H	H
	& Moderate Dead Biomass	10.2	VH	VH	H	H	H	M	H	L
	Extremely High Live Biomass w/ Large Trees & High Dead Biomass	10.3	XH	XH	H	H	VH	VH	H	L
	Extremely High Live Biomass w/ Giant Trees	11	XH	XH	VH	H	H	H	XH	H
	& High Density	11.1	XH	XH	VH	H	H	VH	XH	H
	& Moderate Density	11.2	XH	XH	XH	M	H	M	H	XH

color codes	Very Low	Low	Moderate	High	Very High	Extremely High

Table 2.3. Pearson correlation coefficients for individual structural types with Axes 1 and 2 of a two-dimensional NMS ordination of vegetation zones by structural types.

Structural Type	NMS Axis	
	Axis 1	Axis 2
	r	r
1.1	0.207	0.376
1.2	0.034	-0.223
2.1	-0.375	-0.024
2.2	-0.227	-0.128
3	0.256	-0.227
4	-0.159	-0.033
5.1	-0.156	-0.119
5.2	-0.212	0.032
5.3	0.202	-0.055
6.1	0.026	0.061
6.2	0.212	0.407
7.1	0.153	-0.095
7.2	0.322	-0.034
7.3	0.272	-0.071
8.1	0.256	-0.24
8.2	0.375	-0.271
8.3	0.337	-0.325
9.1	0.347	0.053
9.2	0.395	-0.107
9.3	0.491	-0.062
10.1	0.422	-0.032
10.2	0.435	-0.098
10.3	0.485	-0.287
11.1	0.429	-0.416
11.2	0.397	-0.432

Table 2.4. Characterization of developmental status of the 11 major structural classes and 25 structural types by vegetation zone (Simpson 2013) in the Pacific Northwest. Vegetation zone names are abbreviated: WJ=Western Juniper, PP=Ponderosa Pine, WF/GF=White Fir/Grand Fir, DF=Douglas-fir, SS-RW= Sitka Spruce – Redwood, DF-TO=Douglas-fir – Tanoak, WH=Western Hemlock, SF=Silver Fir, and MH=Mountain Hemlock. Lines of evidence are based on stand age (Age), recent fire history since 1984 (RFH), and productivity (PROD), and management history (HIST), and current management practices (CMP) in each of the corresponding vegetation zones.

Group	Structural Type	Developmental Stage	Potential Disturbance History	Vegetation Zone	Evidence
Low	(1.1) Very Low Live Tree Biomass & Density w/ Very High Snag Density & Biomass	Early	Stand replacing fire and/or epidemic pathogen	ALL	Age, RFH
	(1.2) Very Low Live Tree Biomass & Density w/out Snags		Recent clearcutting, Salvage following recent wildfire and/or epidemic pathogen		Age, RFH
	(2.1) Low Biomass & Density w/ Medium Trees		Aggrading forest		Age, PROD
	(2.2) Low Biomass & Low Density w/ Small Trees		Clearcutting w/ full biomass removal, aggrading forest		Age
	(3.0) Low Biomass & High Density w/ Small Trees		Clearcutting		Age, HIST
			Recent stand replacing fire		RFH
			Aggrading forest		Age, PROD
Moderate	(4.0) Moderate Biomass & Low Density w/ Big Trees	Mid	Variable retention harvest	SS-RW, DF-TO, WH	CMP
		Late	Aggrading forest, Low severity fire	SF, MH, WJ, PP, WF/GF, DF, SA	Age, PROD
	(5.1) Moderate Biomass & Very High Density w/ Medium Trees, (5.3) Moderate Live Biomass & High Density	Mature	Aggrading forest approaching canopy closure	WJ	Age
		Mid	Densified from fire exclusion and high grading	PP, WF/GF, DF	Age, HIST
			Mid/Late 20th century clearcutting	SS-RW, WH	Age, HIST
			Aggrading forest	SF, MH, SA	Age
	(5.2) Moderate Density w/ Medium Trees		Thinning, prescribed fire	PP, WF/GF, DF	Age, CMP
		Mature	Aggrading forest	WJ	Age
	(6.1) Moderate Biomass & Density w/ Big Trees & Moderate Snag Density	Mature	Recent low severity fire, endemic insect and/or disease	SS-RW, DF-TO, WH, SF	Age, RFH
		Late		MH, WF/GF, DF, WJ, PP	
	(6.2) Moderate Biomass & Density w/ Big Trees & Very High Snag Density & Biomass	Early	Recent partial stand replaceming fire and/or epidemic insect, pathogen	ALL	RFH
	(7.1) Moderate Biomass & High Density, (7.2) Moderate Biomass &Very High Density, (7.3) Moderate Biomass & Extremely High Density	Mid	Mid/Late 20th century clearcutting, thinning	WH	Age, HIST
		Mature	Densified from fire exclusion and high grading	PP, WF/GF, DF	Age, HIST
			Long time since stand replacing disturbance, Aggrading forest	SF, MH, SA	Age, PROD
High	(8.1) High Biomass & Density w/ Big Trees w/ Low Dead Biomass	Mature	Early/Mid 20th clearcutting	SS-RW, DF-TO, WH	Age, HIST
		Late	Long time since stand replacing disturbance, Aggrading forest	SF, MH, SA, WF/GF, DF	Age, PROD
	(8.2) High Biomass & Density w/ Big Trees & Very High Biomass of Dead & Downed Wood	Mature	Early/Mid 20th century stand replacing fire	SS-RW, DF-TO, WH	Age, HIST
	(8.3) High Live Biomass & Moderate Density w/ Big Trees		Mid 20th century clearcutting, recent thinning	SS-RW, DF-TO, WH	Age, HIST, CMP
			Mid 20th century clearcutting	RW-SS, DF-TO, WH	Age, HIST
	(9.1) High Biomass & Very High Density w/ Moderate Dead Biomass, (9.2) High Biomass & Very High Density w/ Low Dead Biomass	Late	Recent thinning	WF/GF, DF	Age, HIST, CMP
			Long time since stand replacing disturbance, Aggrading forest	SF, MH, PP, WF/GF, DF, SA	Age, PROD
	(9.3) High Biomass & Extremely High Density w/ High Dead Biomass	Mature	Early 20th century stand replacing fire	RW-SS, DF-TO, WH	Age, HIST
		Late	Late 19th century stand replacing fire	SF, MH, PP, WF/GF, DF, SA	Age, HIST
	(10.1) Very High Biomass & High Density w/ Large Trees w/ High Dead Biomass & Understory Cover	Mature	Centuries since stand replacing disturbance	SS-RW, DF-TO, WH, SF	Age
		Late		MH, WF/GF, DF, SA	
	(10.2) Very High Biomass & High Density w/ Large Trees w/ Moderate Dead Biomass	Mature		SS-RW, DF-TO, WH, SF	
		Late		MH, PP, WF/GF, DF, SA	
	(10.3) Extremely High Live Biomass w/ High Dead Biomass			SS-RW, DF-TO, WH, SF, MH, WF/GF, DF	
	(11.1) Extremely High Live Biomass w/ Giant Trees & High Density, (11.2) Extremely High Live Biomass w/ Giant Trees & Moderate Density				

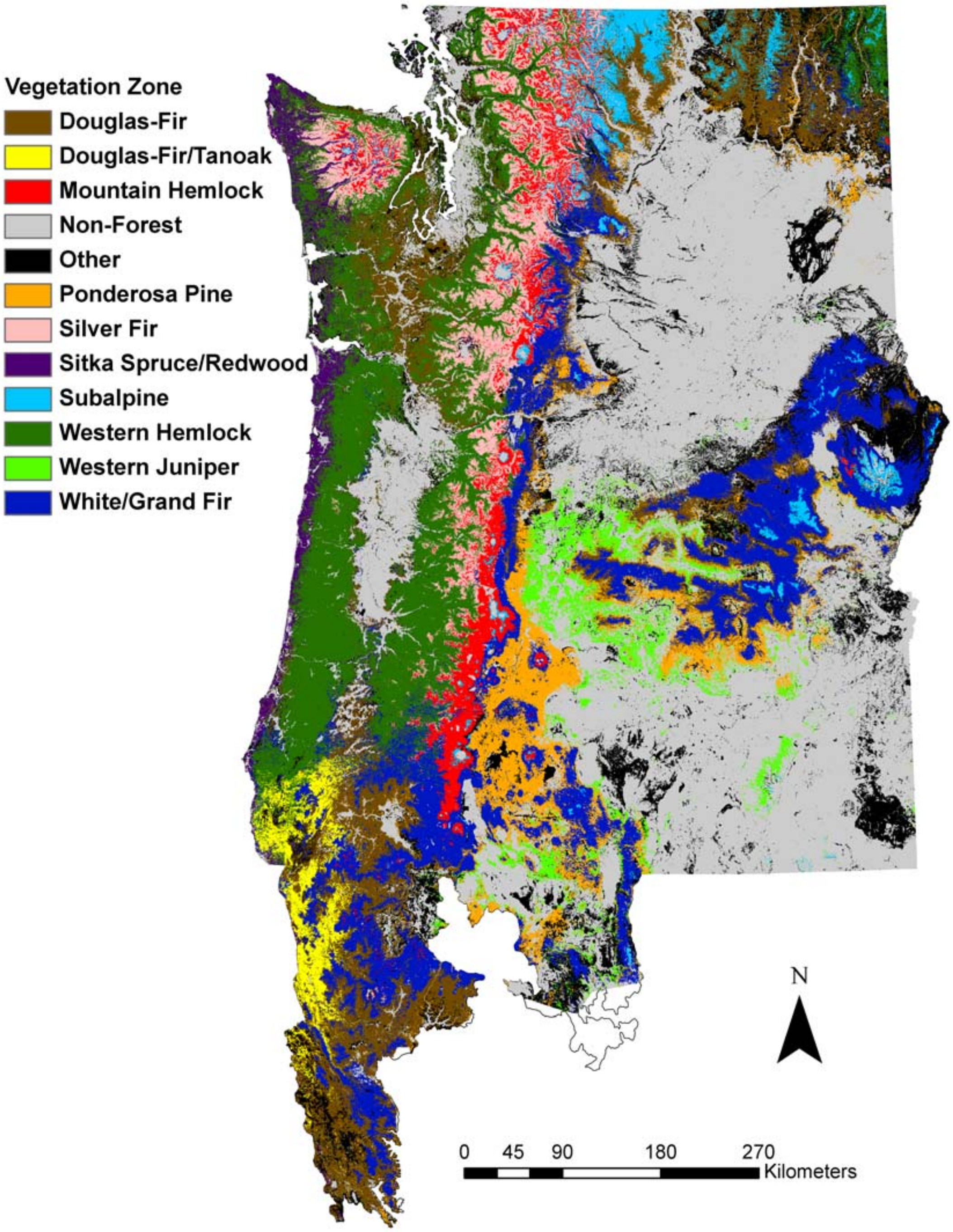


Figure 2.1. Map of major forested potential vegetation types (from Simpson 2013) in Oregon, Washington, and inland Northern California.

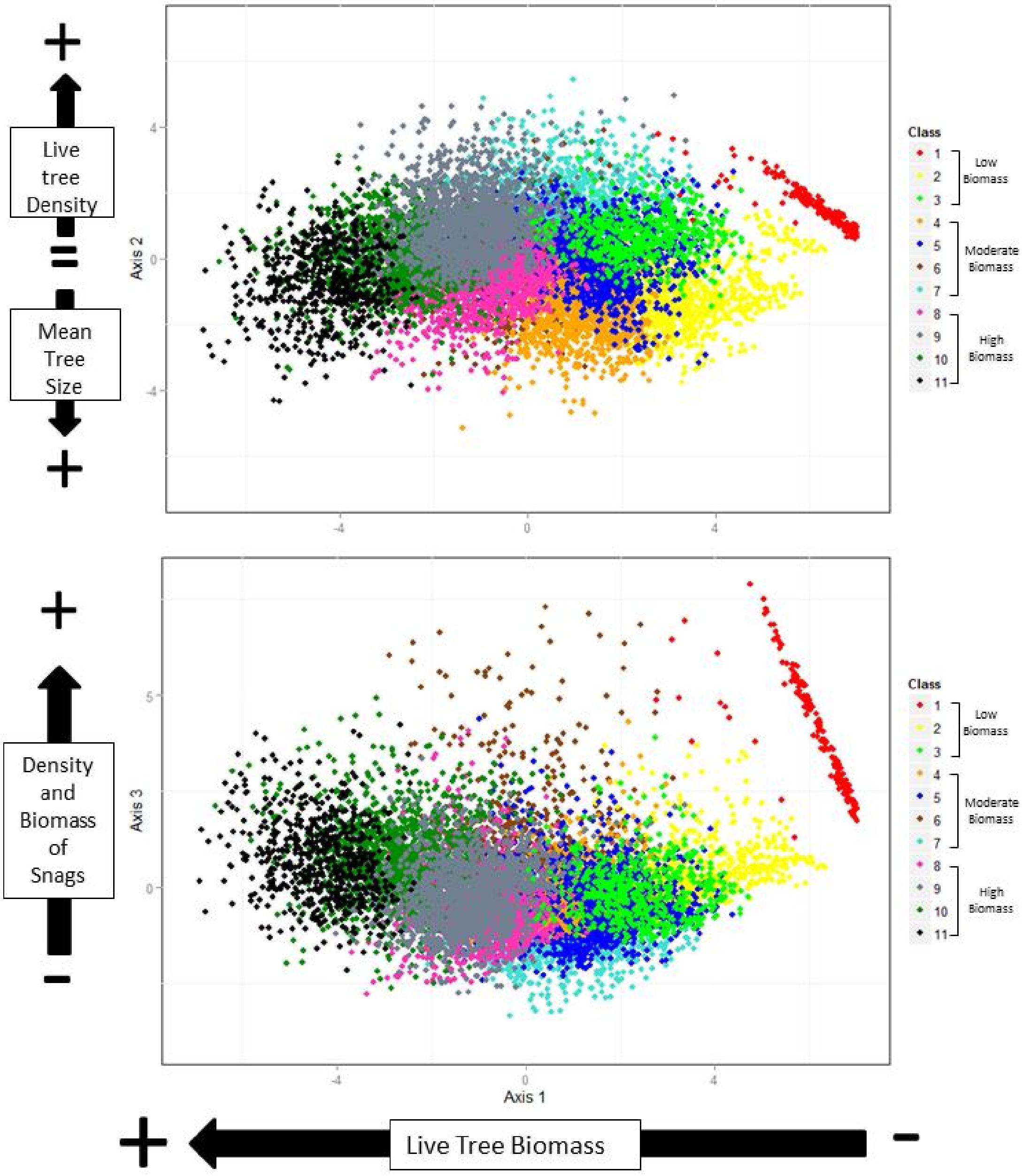


Figure 2.2. Principal components analysis ordination representing the first three axes of forest structural variation in the Pacific Northwest with 11 major structural classes overlain on a) Axis 1 vs Axis 2 and b) Axis 1 vs. 3.

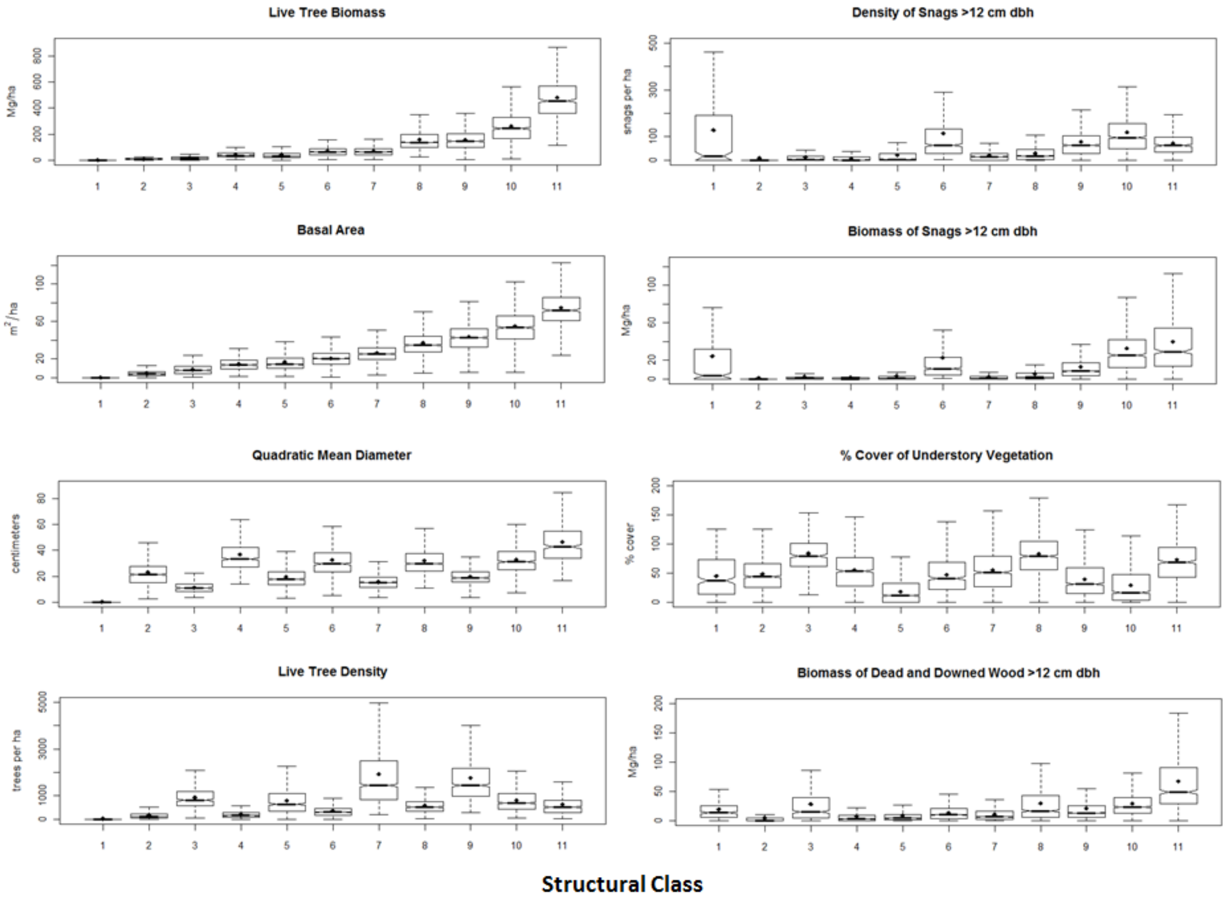
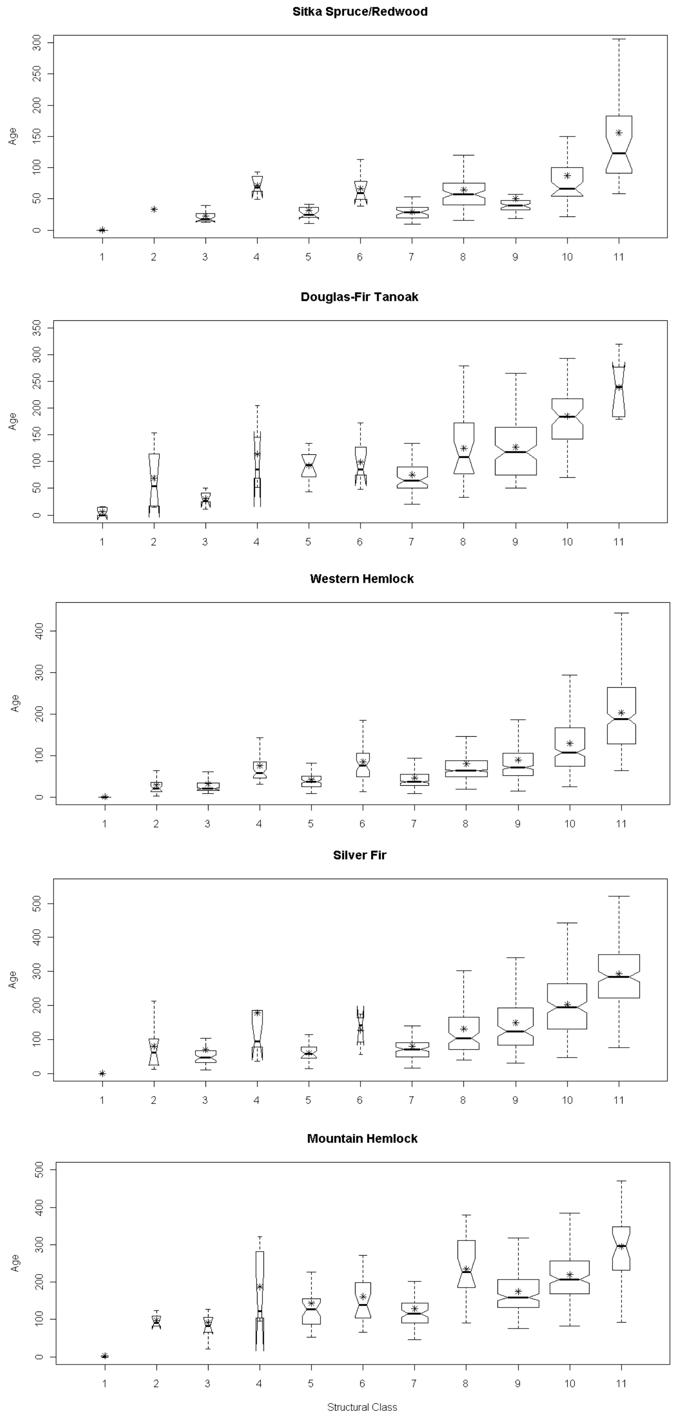


Figure 2.3. Boxplots of eight of the variables used in the hierarchical classification of forest structure in the Pacific Northwest for eleven major structural classes.



Sitka Spruce/Redwood

Douglas-Fir Tanoak

Western Hemlock

Silver Fir

Mountain Hemlock

Figure 2.4. Boxplots of mean age of all dominant and co-dominant trees by structural class for wet vegetation zones including a) Sitka-spruce/redwood, b) Douglas-fir tanoak, c) western hemlock, d) silver fir, and e) mountain hemlock. The width of each boxplot is proportional to the square root of the sample size and means are represented by an *.

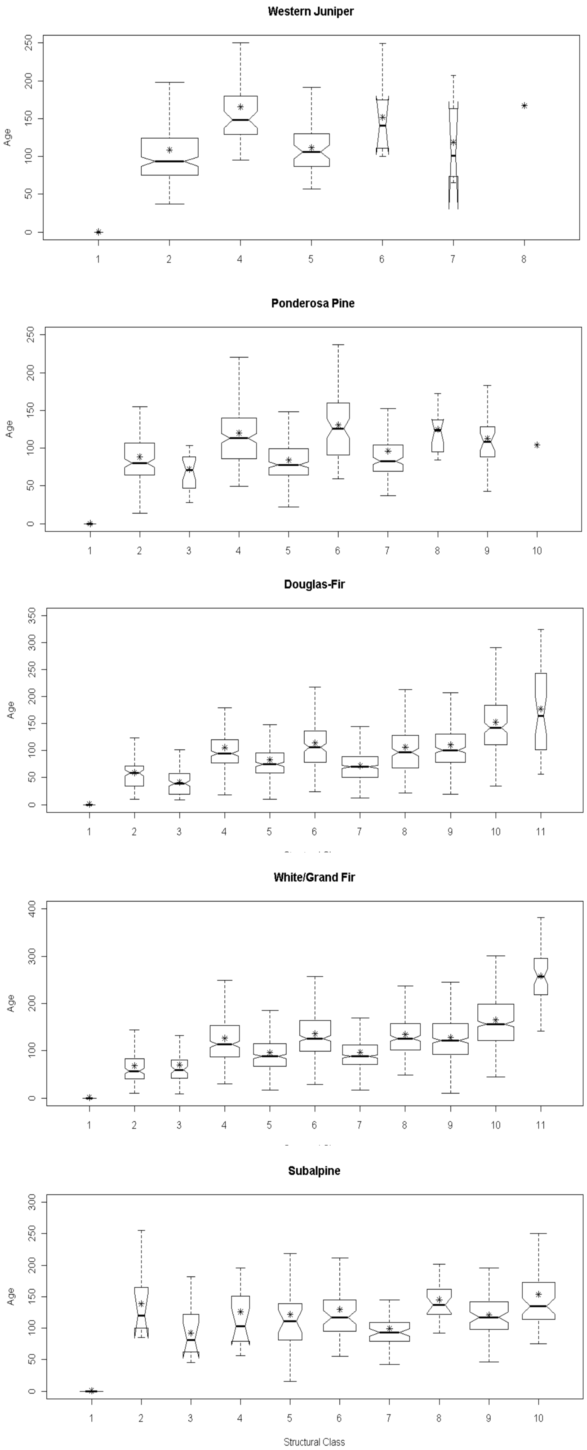
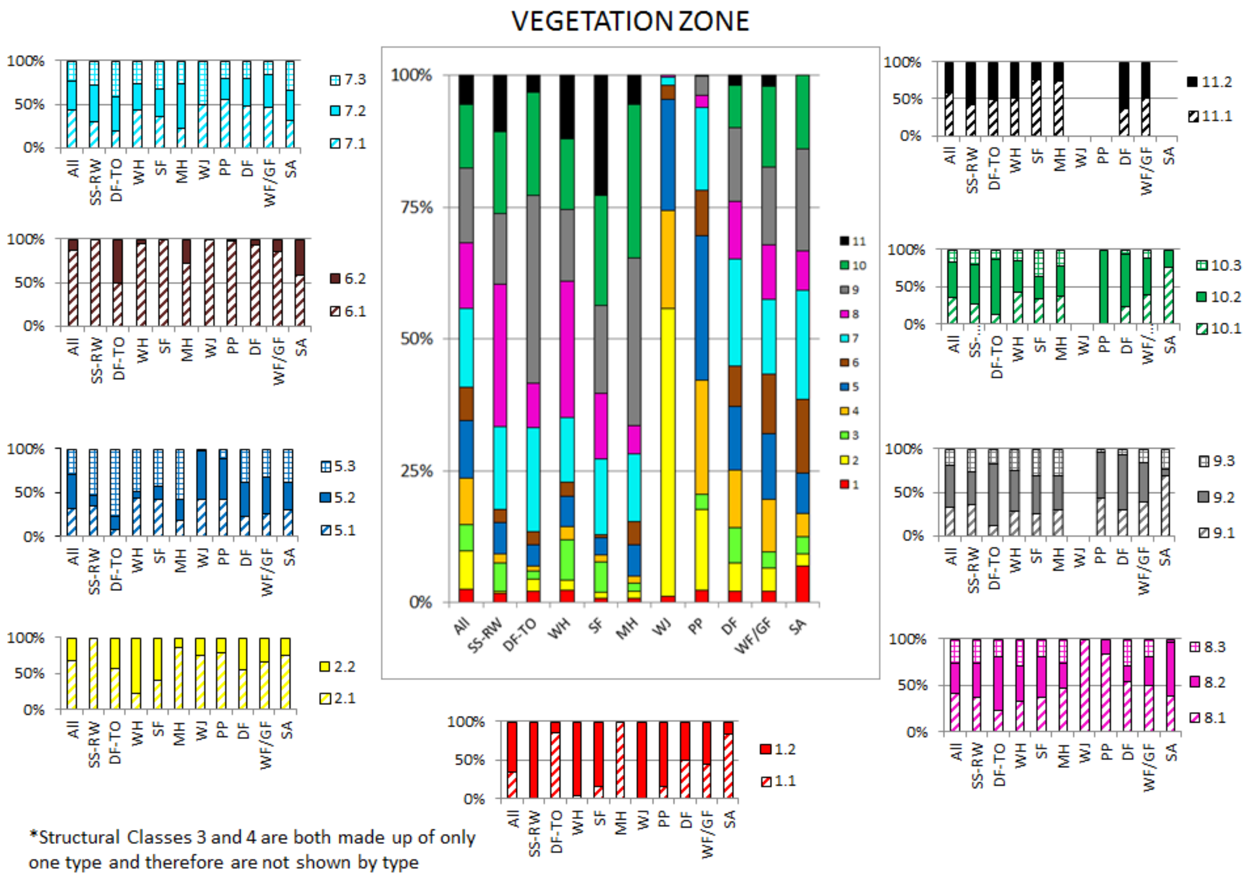


Figure 2.5. Boxplots of mean age of all dominant and co-dominant trees by structural class for dry vegetation zones including a) western juniper, b) ponderosa pine, c) Douglas-fir, d) grand fir, and e) subalpine forests. The width of each boxplot is proportional to the square root of the sample size and means are represented by an *.



*Structural Classes 3 and 4 are both made up of only one type and therefore are not shown by type

Figure 2.6. Relative abundance of major structural classes and types in forests of the Pacific Northwest by vegetation zone. Vegetation zone names are abbreviated: WJ=Western Juniper, PP=Ponderosa Pine, WF/GF=White/Grand Fir, DF=Douglas-fir, SS-RW= Sitka Spruce – Redwood, DF-TO=Douglas-fir – Tanoak, WH=Western Hemlock, SF=Silver Fir, and MH=Mountain Hemlock.

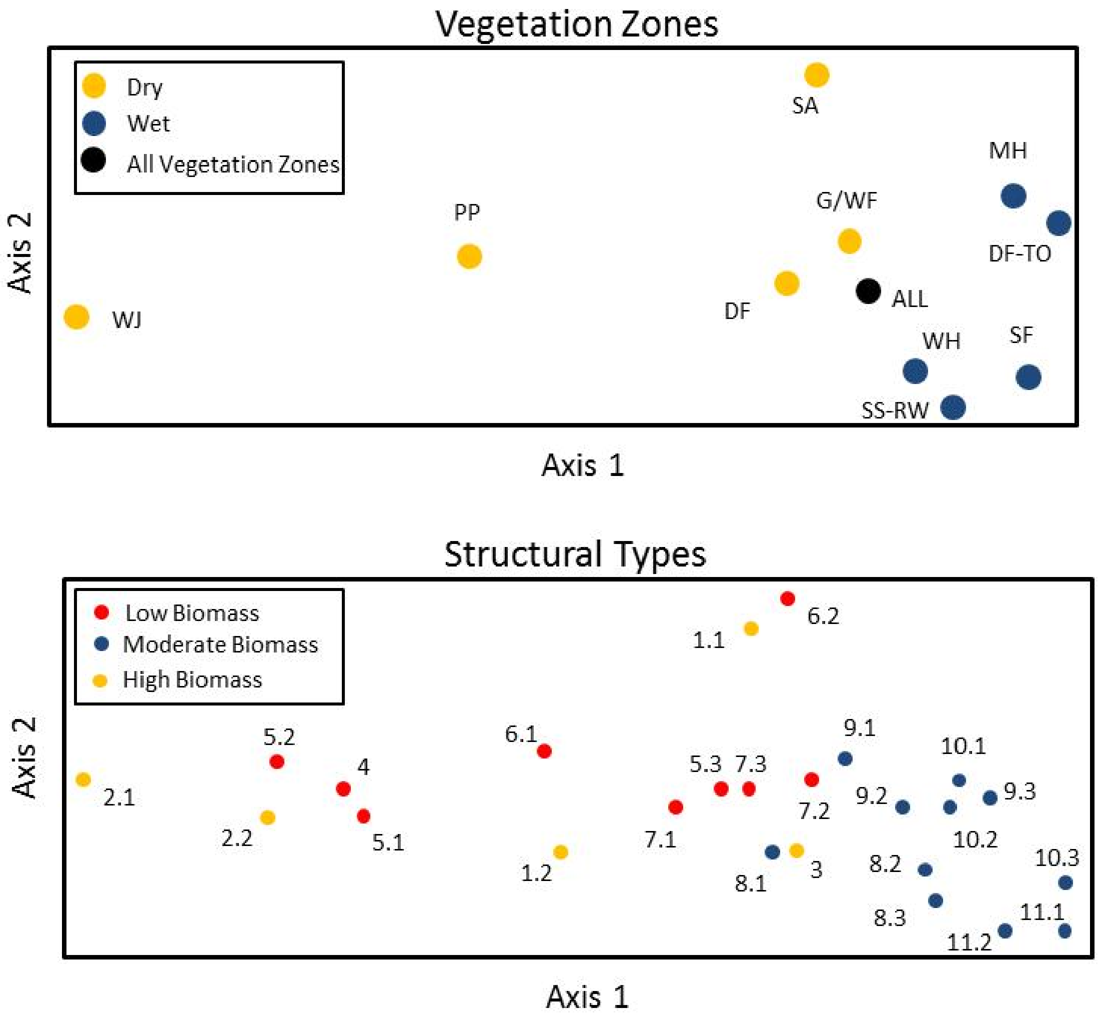


Figure 2.7. NMS ordination of the relative abundance of structural types by vegetation zone with a) vegetation zones and b) structural type overlays. Vegetation zone names are abbreviated: WJ=Western Juniper, PP=Ponderosa Pine, WF/GF=White/Grand Fir, DF=Douglas-fir, SS-RW= Sitka Spruce – Redwood, DF-TO=Douglas-fir – Tanoak, WH=Western Hemlock, SF=Silver Fir, and MH=Mountain Hemlock.

Chapter 3: Variation in stand-level tree mortality and structural development in forests of the Pacific Northwest

Abstract

Recent studies have documented widespread tree mortality associated with increased drought and wildfire across the globe. However, the ecological effects of mortality as a demographic process are poorly understood and we lack knowledge of the regional distribution of mortality rates and associated change in forest structure. I used data from 3,673 forest inventory plots to examine short interval (4-14 years) mortality rates from the mid-1990’s to the mid-2000’s, a period with extreme drought and the occurrence of multiple large wildfires, across 11 million ha in the Pacific Northwest. Almost half of all plots were within the range of background tree mortality rates reported in other studies (<1.0 %/yr) and extremely high levels of mortality (≥25%/yr) were rare. However, rates in approximately half of the plots fell in between, indicating that a classification of mortality into background and stand-replacement is insufficient to represent regional scale dynamics. The distributions of mortality differed among many vegetation zones. Levels of mortality were primarily <2.5%/yr in western hemlock, silver fir, and mountain hemlock vegetation zones where fires were rare and insects and pathogens occurred predominantly at endemic levels. Rates were highest in subalpine forests and higher elevation grand fir and Douglas-fir forests as a result of fire and insects. Mortality rates in the hottest driest forest vegetation zone, ponderosa pine, were surprisingly low, especially in undisturbed forests where there was little to no mortality. Mortality rates varied among developmental stages in all vegetation zones and few

consistent patterns emerged. Levels of mortality were often lowest in early developmental stages but varied in later stages. Application of a simple framework indicated that multiple trajectories of structural change were common at levels of mortality <2.5%/yr, but structural change at higher levels was predominantly associated with decreases in density and increases in mean tree size. Results indicate that the rate and magnitude of forest change associated with mortality varies widely across the region. In vegetation zones where disturbances such as insects and fire are widespread, change has occurred much more rapidly and restored some aspects of historical structure by decreasing overall density and increasing the dominance of big trees. In other vegetation zones where higher levels of mortality were rare, structural change was more subtle and may take longer periods of time for substantial change to occur. This examination of short-period mortality rates and associated structural change across a broad geographic extent provides context for understanding trends from localized studies and potential ecological consequences of mortality.

Introduction

Tree mortality is a primary driver of structure and function in forested ecosystems worldwide (Franklin et al. 1987). As a demographic process, mortality shapes tree population structure (Harcombe 1987, Coomes and Allen 2007) and subsequently influences stand-level structure, composition, and successional change (Peet and Christensen 1980). Tree mortality has recently emerged as a major focus of ecological research around the world following the occurrence of large scale "die-off" in forests all over the world as a result of increased temperatures and drought (Allen et al. 2010, Williams et al. 2010, Martinez-Carnicier et al. 2011, Martinez-Vilalta et a. 2013), but few studies have actually investigated the patterns and consequences of mortality in an ecological context (Anderegg et al. 2013). Future climate projections suggest that major changes in forest composition and structure will likely occur as a result of widespread tree mortality (Williams et al. 2010), yet we currently lack a general characterization of the associated ecological effects of mortality across forests differing environment and age classes.

Previous ecological investigations of tree mortality have primarily been longitudinal studies in old, unmanaged forests focused on documenting "background" rates as a baseline with which to compare future change (e.g. Phillips et al. 2004, van Mantgem et al. 2009). Background mortality generally refers to low, relatively stable rates of mortality associated with endogenous fine-scale processes such as density dependent thinning, resulting from competition for resources or senescence of older trees (Chen et al. 2008). Stand-level tree mortality rates in old-growth forests range from <1 to

1.5 %/year in temperate forests (Abrell et al. 1977, Parker et al. 1985, Bible 2001, van Mantgem et al. 2009, Larson and Franklin 2010), increase with productivity (Stevenson et al. 2012) and can be as much as 3 %/year (Swaine et al. 1987, Condit et al. 1995, Thomas et al. 2013) in tropical forests. Recent work suggests that background mortality rates are increasing in both temperate and tropical forests as a result of warming, drought, and increasing levels of atmospheric CO_2 (Gentry and Phillips, 1994, Phillips et al. 2004, Stephenson and van Mantgem 2005, van Mantgem et al 2009, Peng et al. 2011), but there is much uncertainty and confusion distinguishing between the effects of mortality associated with stand development processes and those associated with exogenous stress induced by climate (van Mantgem et al 2009, Peng et al. 2011, Luo and Chen 2013).

Despite its usefulness as a baseline with which to compare future changes, the concept of background mortality is insufficient to represent variation in tree mortality across larger spatial scales where a variety of natural disturbances may be operating (Lugo and Scatena 1996, Vanderwel et al. 2013). While small changes in background mortality rates can alter stand structure over long time scales (Pacala et al. 1996), disturbances have the potential to rapidly alter forest stand structure over much shorter time scales (Lugo and Scatena 1996). “Pulse” disturbances such as wildfires and wind include discrete events that may be stand-replacing and reset structural development and succession. Such changes in structure are rapid but can have effects that persist for decades to centuries (Gray and Franklin 1997). Other biotic disturbances include insects, disease, and pathogens, all of which are often associated with drought and can be classified as “press” disturbances where mortality remains elevated above normal background levels for an extended period.

Tree mortality operates throughout most stages of structural development, but it is generally thought to be highest in early and middle stages of structural development and lowest in later stages (Peet and Christensen 1980, Franklin et al. 2002). Studies of mortality in early and mid developmental stages are less common than those in later stages, but recent studies support this hypothesis (Bible 2001, Chazdon 2005, Lutz and Halpern 2006, Luo and Chen 2013). However, mortality may be low during early developmental stages in forests where density dependent mortality may not occur as a result of previous management (e.g. mechanical thinning) or in those undergoing protracted establishment at lower density (Franklin et al. 2002). Relatively high levels of density dependent mortality associated with competition are hypothesized to decrease over time and stabilize in older stands as mortality shifts towards density independent causes associated with disturbance agents such as wind, disease, and insects (Franklin et al. 2002). There is some evidence supporting this hypothesis (Bible 2001, Luo and Chen 2013), but studies comparing mortality among a broad range of stand ages are rare and limited to a few systems.

Understanding the effects of tree mortality on structural developmental has the potential to clarify much of the uncertainty regarding the roles of developmental processes and exogenous factors (e.g. fire, climate change) (van Mantgem et al 2009, Peng et al. 2011, Luo and Chen 2013). Multiple pathways of structural development have been documented in many forests and can vary depending on disturbance and developmental stage (Fastie 1995, Zenner 2005, Frelich 2008, Tepley et al. 2013). Coomes and Allen (2007) provide a generalized framework for examining structural change that I expand on in this paper where stands may be classified into one of four trajectories of structural development over a period of observation depending on various combinations of increases and decreases in the density and size of trees (Fig. 3.1). "Densifying" forests include those where density increases and mean tree size decreases as a result of recruitment of smaller trees and potentially mortality of larger trees. "Aggrading" forests include those where density and mean tree size increase as a result of growth and recruitment. Forests classified as "thinning" (Coomes and Allen 2007) have decrease in density and increase in tree size when mortality operates primarily on smaller trees and increases the dominance of larger trees (Oliver and Larson 1990). Finally, forests experiencing "die-back" exhibit decreases in mean tree size and density as a result of mortality of larger trees (Mueller-Dombois 1987) with little recruitment of smaller trees.

Given recent and predicted future forest die-off from warming and drought (Williams et al. 2012) and increased frequency of wildfires (Westerling et al. 2006), there is a growing need for empirical information to help us understand regional variation in the ecological effects of tree mortality to inform management and policy. Previous studies of forest dynamics at broad scales have traditionally been conducted at correspondingly long times scales (Delcourt et al. 1983, Delcourt and Delcourt 1988), but recent work suggests short term observations may be necessary for understanding dynamics during times of rapid change (Allen and Breshears 1998). Increasing evidence that forests are undergoing rapid ecological change as a result of tree mortality underlies the need not only to document variation in stand level mortality rates at short intervals at a range of spatial scales, but to interpret variation in mortality rates and associated structural change in forests that differ in age and productivity. Similar mortality rates will likely have different ecological effects as result of variation in growth and recruitment during different developmental stages and at different levels of productivity. Characterizing this variation will inform our understanding of the magnitude and extent of tree mortality effects on regional biodiversity and the potential resilience and recovery in various vegetation zones.

I used repeat observations on 3,673 forest inventory plots across an 11 million ha study area in the Pacific Northwest to examine variation in stand-level rates of tree mortality from the mid-1990's to the mid-2000's. During this period the study region experienced centennial scale mega-drought (Schwalm et al. 2012) accompanied by an increase in background mortality rates of trees of old-growth forests (van Mantgem et al. 2009) and an increase in area burned by wildfire (Littell et al. 2009). I compare the distributions of short interval (4-14 years) mortality rates and among different disturbances, vegetation zones, and stages of structural development and test the following three main hypotheses:

1) Distributions of mortality rates are characterized by a peak at low levels in undisturbed forests, but have a long tail and shift to higher levels in forests where disturbances have occurred. Mortality levels are lowest in forests affected by pathogens, followed by insects and wind which cover a range of intermediate levels of mortality, and

highest in fires where stand-replacing events result in a long tail at high levels of mortality.

2) Distributions of mortality rates differ among vegetation zones. Mortality rates in undisturbed wet vegetation zones are higher than those in lower productivity cold and dry vegetation zones, but cold and dry vegetation zones have a greater proportion of plots with higher levels of mortality from insects and wildfire associated with hot dry conditions during the study period.

3) Early and middle stages of structural development have higher levels of mortality than later developmental stages. Greater density dependent mortality associated with competition early in structural development results in more mortality than in later stages when mortality is generally low and related to the occurrence of small scale disturbances (e.g. single tree canopy gaps)

I then use the previously described framework to characterize recent trajectories of structural change and examine how the prevalence of each trajectory varies across different levels of mortality and stages of structural development (Fig. 3.1). This framework reduces potential pathways of structural development into four trajectories defined by changes in live tree density and mean tree size. Different drivers of mortality (e.g. density dependent competition, disturbance) may cause similar levels of mortality, but their effects on stand structure may manifest themselves in different ways, resulting in multiple pathways of development. Assessing the prevalence of different trajectories at different levels of mortality can reveal larger scale trends in dynamics of individual vegetation zones or particular stages of structural development.

Methods

Study Region

My study region is approximately 11 million ha (Figure 3.2) and includes all lands administered in Oregon and Washington by the United States Forest Service Pacific Northwest Region. The region is highly diverse including a wide variety of potential vegetation types due to strong climatic and topographic gradients (Franklin and Dyrness 1973). Potential Vegetation Types (PVTs) represent physical environments and geographic ranges distinguished by the tree species that would dominate in later developmental stages in the absence of stand replacing disturbance (Pfister and Arno 1980). I acquired a PVT map of Oregon and Washington from the Ecoshare Interagency Clearinghouse of Ecological Information (www.ecoshare.info/category/gis-data-vegzones). The map was created following Henderson et al. (2011) using existing forest inventory data on species distributions in relation to dominant climatic and topographic gradients. I grouped these into wet, cold, and dry environments for the purpose of analyzing mortality patterns. Wet forests include western hemlock (*Tsuga heterophylla*) and silver fir (*Abies amabilis*) PVTs. Cold forests include mountain hemlock (*Tsuga mertensiana*), subalpine fir (*Abies lasiocarpa*), and subalpine parklands dominated by whitebark pine (*Pinus albicaulis*). I combined subalpine fir and subalpine parklands into one PVT which we refer to as subalpine. Dry forest PVTs include ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Psuedostuga menziziii*), and grand fir/white fir (*Abies grandis/concolor).*

Natural and anthropogenic disturbances have influenced the development of forest structure in all vegetation zones. Wildfire played a major role across the entire study region at different time periods (Agee 1993). Historic fire regimes range from high frequency, low severity fire in warm, dry forests to low frequency, high severity fire on cold and wet forests. Much of the vegetation in the region was historically subject to a mixed severity fire regime where the proportion of high severity fire varied spatially and temporally (Agee 1993). Long periods of fire exclusion are believed to have altered forest composition and structure across much of the region, particularly in dry forests of the eastern and southern portions of the region (Perry et al. 2011), but wildfires have increased in frequency and extent since the mid-1950s (Littell et al. 2009). Windstorms and landslides associated with storms off the Pacific Ocean play a far greater role in wet forests than in dry forests, particularly on steep, exposed landforms (Sinton et al. 2000).

Field Data

I acquired field data from the Current Vegetation Survey (CVS) inventory of USDA Forest Service Region 6 (R6). The CVS is a region wide vegetation monitoring program with plots located on a 2.5 by 2.5 km grid across all the national forest lands in Oregon and Washington, with the exception of federally designated wilderness areas where plots are located every 5 km (Fig. 3.2). The CVS data set consists of over 11,000 plots measured on two occasions, first between 1992 and 1997 and second between 1997 and 2007. Sampling intervals range from one year to fourteen years, but I limited my sample to those plots with $\geq$ 20 live tagged trees and an interval $\geq$ 4 years between sampling and no evidence of logging during the intervals, limiting potential sources of mortality to those of natural causes. This reduced the initial sample to 3,673 plots with 289,390 tagged trees.

The CVS plot design includes a series of four variable radius subplots ranging nested within a circular 1 ha plot. At each subplot center, located 40.8 m from the center of the 1 ha plot, a series of nested variable radius subplots was established. In the first subplot (0.004 ha) all live trees 7.6-12.4 cm diameter at breast height (dbh) within 3.6 m of the stake were identified, measured for dbh, and tagged. In the second subplot (0.017 ha) all live trees 7.6- 32.8 cm dbh within a 7.3 m radius of the subplot center were identified, measured for dbh, and tagged. Data collection in the third subplot, which differed between the east and west sides of the Cascade Crest, focused on large trees. On the westside, all live trees 32.9-121.7 cm dbh within a 15.6 m radius (0.4 ha) of the subplot center were identified, measured for dbh, and tagged. On the east side all live trees and snags 32.9-81 cm dbh within a 15.6 m radius (0.4 ha) of the subplot center were identified, measured for dbh, and tagged. Finally, all live trees >121.7 cm on the west side and all trees >81 cm dbh on the east side were identified, measured for dbh, and tagged across the entire 1 ha plot.

I used narratives written at installation and again at re-measurement on the present condition and past disturbance (PCPD) of each plot to record the occurrence of specific disturbances during the re-measurement interval. Field protocols specified noting specific disturbances including disease/pathogen and insects, wind throw, fire, and wildlife, but other disturbances including avalanches, flooding, landslides, falling rocks, and were also documented in the narratives. I reviewed all narratives and recorded specific reference to each of the following disturbances occurring within the plot during the sampling interval: pathogen/disease, insects, fire, wind, snow/weather, flooding, avalanche, falling rocks, landslides, and wildlife. I also recorded past wildfires that were mentioned and occurred within 15 years prior to sampling. I treated the data as a presence/absence indicator of disturbance occurrence with no interpretation of severity to avoid field recorder bias.

I used randomForest in R to classify plots into several structural classes representing early, mid, mature, late, and old-growth developmental stages following a pre-existing classification of forests structure based on several attributes of forest structure (This dissertation, Chapter 2). Classification accuracy was approximately 80% at the class level and error ranged from a high of 25.9% to a low of 1.8% (Appendix: Table A-2.1).

Data Analysis

I calculated annualized mortality rates following Sheil et al. (1995) using the following equation:

$$m = 1-(1-((N_{t1}-N_{t2})/N_{t1})^{(1/t)}$$

where N_{t1}=number of live trees at initial sampling, N_{t2}=number of trees that survived until the second sampling, and t=number of years between first and second sampling.

I tested for differences in the cumulative distribution function of mortality rates among disturbances and vegetation zones based on an F-distribution version of the Wald statistic (Kincaid 2000) using the cont.cdftest in the package spsurvey (R version 2.13.2). I adjusted p-values (Verhoeven et al. 2005) using the package fdr.tools to account for false discovery rate (Benjamini and Hochberg in 1995) and reduce the potential for Type II errors associated with the large number of comparisons,.

Plots were classified in to one of four potential trajectories of structural change (Fig. 3.1) based on changes in quadratic mean diameter(QMD) and density of trees per ha (TPH) according to the following rules: 1)"densifying": ΔTPH$\geq$0 and ΔQMD <0, 2) "aggrading": ΔTPH $\geq$0 and ΔQMD $\geq$0, 3) "die-back": ΔTPH <0 and ΔQMD <0, and 4)"thinning": ΔTPH<0 and ΔQMD>0. I then plotted quadratic mean diameter (QMD) and trees per hectare (TPH) at initial and second sampling and examined vectors of change between sampling periods to assess patterns of structural development at various levels of mortality in individual vegetation zones forests.

Results

Distribution of Mortality Rates by Disturbance

I found significant differences ($p<0.05$) between the cumulative distribution functions of tree mortality rates between most disturbances (Fig. 3.3, Appendix: Table A-2.2). Plots with no evidence of disturbance had the lowest levels of mortality overall. Mortality in plots with pathogens occurred at higher levels than plots with no disturbance, but was lower than in plots with evidence of both pathogens and insects or insects alone which did not differ. Plots with evidence of wind had the highest proportion of plots in the middle of the range but were rarely >10%/yr. Plots with evidence of insects and fire and fire alone generally spanned the entire range of rates and accounted for the highest levels of mortality. Plots with evidence of fire alone did not differ from those with fire and insects, but those with fire alone had a much higher proportion of rates at 100%/yr.

Distribution of Mortality Rates by Vegetation Zone

I found significant difference between the cumulative distribution functions of tree mortality rates of most major vegetation zones (Fig. 3.4, Appendix: Table A-2.3) with exception of western hemlock and silver fir, silver fir and mountain hemlock, and subalpine and grand/white fir. Distributions in wet and cold forests were somewhat normal with varying degrees of skewness but resembled a negative exponential distribution in very dry forests. Western hemlock differed from all vegetation zones except silver fir and both had the highest proportions of rates in the 1-2.5% yr range and the lowest proportions of rates >5%/yr. Mountain hemlock differed from all vegetation zones except silver fir and had the lowest proportion of plots with no mortality. Subalpine forests differed from all vegetation zones except grand fir, both of which had relatively high proportions of rates >5%/yr. Douglas-fir forests differed from all vegetation zones and had a relatively high proportion of plots with mortality rates <1%/yr, but also a relatively high proportion of rates >5%/yr. The distribution of mortality rates in ponderosa pine differed from all other vegetation zones and had the highest proportion of plots with very low or no mortality and a small proportion at rates >10%/yr.

Distribution of Mortality Rates by Developmental Stage

I found significant differences between the cumulative distribution functions of tree mortality rates among developmental stages within all the major vegetation zones (Fig. 3.5, Fig. 3.6, Fig.3.7, Appendix: Tables A-2.4 thru A-2.10), but there were few consistent differences between developmental stages across all vegetation zones. Early development stages in western hemlock had a high proportion of rates <1%/yr, while later developmental stages had much greater proportions of mortality >1%/yr, but cumulative distributions frequently differed between stages. Early development stages in silver fir also had high proportion of rates <1%/yr, but differed only from the late developmental stage which, along with the mature stage, had the greatest proportions of rates >1.75%/yr. In mountain hemlock there was a general shift to higher levels of mortality in later developmental stages, but the only statistically significant difference was between early and old-growth stages. This pattern was similar but stronger in subalpine forests, where there were more differences between earlier and later stages. In grand fir, Douglas-fir, and ponderosa pine, there were generally greater proportions with mortality rates >2.5%/yr and lower proportions of rates <1%/yr in late and old growth stages than in mature and mid stages which differed consistently within individual vegetation zones.

Trajectories of Structural Change

Eighteen percent of forests were classified as densifying, 19% as aggrading, 58% as thinning, and 5% as die-back (Table 3.1), but proportions varied by vegetation zone, mortality level, and developmental stage (Appendix: Tables A-2.11 thru A-2.17). The proportion of densifying and aggrading forests decreased rapidly as level of mortality increased in all vegetation zones. Most rates were <2.5%/yr (Fig. 3.8) and pathogens and insects were common in both (Fig. 3.9, Fig. 3.10). Thinning (Fig. 3.11) occurred at all levels of mortality and was the most common trajectory at levels of mortality >1%/yr and <25%/yr (Fig. 3.8). Die-back (Fig. 3.12) occurred across all levels of mortality but was more prevalent at mortality levels >5%/yr and often occurred in approximately half of all plots at levels ≥25%/yr. Insects and pathogens were common at mortality levels <5%/yr in thinning and die-back, but fire was the primary agent of disturbance at levels >10%/yr. The proportion of plots that were thinning increased in later developmental stages while the proportion that were aggrading decreased in all vegetation zones (Fig. 3.13). Die-back occurred more in later developmental stages but varied some among vegetation zones.

Discussion

This study is the first regional-scale characterization of short-interval (4-14 years) tree mortality rates and corresponding effects of forest structural change across multiple vegetation zones of all ages and stages of structural development. The field-based results presented here compliment previous remote sensing based studies of patterns and rates of forest change at large spatial scales (e.g. Breshears et al. 2005, Healy et al. 2008, Williams et al. 2010), but offer increased ecological resolution by characterizing structural change associated with various levels of mortality. Short interval mortality rates were highly variable and ranged from 0 to 100%. Almost half of all plots in most vegetation zones were within the range reported in studies of background mortality in old-growth wet forests of the region (<1.0 %/yr) [Franklin and DeBell 1988 (0.75%.yr), Edmunds et al. 1993 (0.8-0.9%/yr), Bible 2001 (0.5-0.7%/yr), Larson and Franklin 2010 (0.3-0.8%/yr), Lutz et al. 2014 (1.1%/yr)] and extremely high mortality rates (≥25%/yr) were generally rare and restricted to wildfire. However, mortality rates at levels between low and extremely high occurred in almost half of the plots indicating that a simple classification of mortality into background and stand-replacement does not fully represent the range of forest dynamics at a regional scale.

Disturbance and Mortality

Attributing mortality to any single disturbance or agent and distinguishing between proximate and ultimate causes of mortality is often difficult as many interact (Manion 1981) and predispose trees to mortality from other subsequent disturbances (Veblen et al. 1994, Bigler et al. 2005, Larson and Franklin 2010). This poses a limitation on drawing inference to attributing disturbance to individual plots, but still provides valuable insights in to the range of mortality levels across which individual and multiple disturbances occur. Undisturbed plots serve as a baseline distribution to compare to those of individual disturbances, while plots with multiple disturbances (e.g. insects/pathogens and fire/insects) may be compared to that of individual agents to understand how the occurrence of multiple disturbances may shift the distribution of mortality rates. In general, larger proportions of plots occurred at higher levels of mortality in a distinct order with pathogens at the low end, followed by insects, then wind, and finally fire.

Not surprisingly, mortality rates in undisturbed plots were consistently lower than those in plots with evidence of disturbance. However, undisturbed plots in wet and cold vegetation zones had higher levels of mortality than did undisturbed plots in dry vegetation zones. These results are consistent with the results of others who have found that mortality rates in undisturbed forests increase with productivity, presumably as a result of higher levels of competition and greater density dependent mortality

(Stephenson et al. 2011). Despite lower productivity in cold vegetation zones due to a shorter growing season (Hansen-Bristow et al. 1988), “undisturbed” plots in mountain hemlock and subalpine forests had comparatively high rates of mortality as in higher productivity wet forests. This could potentially be explained by chronic weather-related physical damage (e.g. frost, snow loading) (Ives and Hansen-Bristow 1983) that were not specified or detected in my disturbance attribution. Mortality rates in the dry vegetation zones, particularly western juniper and ponderosa pine, were low with large proportions of plots occurring at levels <0.5%/yr. In these vegetation zones where tree density is generally low (This dissertation, Chapter 2), competitive interactions and density dependence may be less important than in wet or cold vegetation zones.

Pathogens and insects were the most common disturbances in almost all vegetation zones, but operated primarily at levels of mortality <2.5%/yr. The considerable overlap between tree mortality distributions in plots affected by insects or pathogens and undisturbed plots indicates that these agents operate primarily at low endemic rates where their effects are similar to those associated with competition. Although these agents may not result in immediate mortality, their effects may manifest themselves initially as decreases in growth and vigor (Cherubini et al. 2002, Marias et al. 2014), but later as part of a long process of mortality (Manion 1981) that can predispose trees to stem breakage or tip-up later in life (Larson and Franklin 2010). In addition, pathogens and diseases can have complex relationships that can further increase probability of tree mortality (Raffa et al. 2005). My results suggest that the presence of insects can shift mortality in stands to higher levels of mortality than those occurring in plots with pathogens alone, but that stands with both are not likely subject to higher levels of mortality than those with just insects. Although many forests in western North America have experienced recent mortality from insects (Raffa et al. 2008), actual mortality rates in the Pacific Northwest very rarely exceeded 10%/yr during the study period. Part of this might be explained by the fact that most insects are species specific, thus not all trees in mixed species stands are susceptible. It is also possible that the occurrence of fire may mask the presence of insect-related mortality during the study interval. Either way, outbreaks of insects and pathogens appear to operate more as "press" disturbances where levels of mortality are elevated above those in undisturbed forests for extended periods. In these cases, the duration of the episode may be at least as important as the mortality rate, particularly when outbreaks are associated with extended drought (Bigler et al. 2007, Carnicer et al. 2011).

Plots where wind disturbance was recorded had greater proportions at higher levels of mortality than insects and pathogens, primarily at levels in the 1-10%/yr range. At lower levels of mortality wind may operate selectively on single or a few larger trees that can cause additional mortality by crushing of smaller trees (Putz et al. 1983). This may occur as an isolated pulse disturbance event, but wind may also operate as a push disturbance and have chronic effects (Mitchell 2012). The long term effects of pathogens and disease may decrease stability and predispose some trees for tip up or snapping which can initiate a period of elevated mortality in places where wind is chronic (Worrall et al. 2004). This process is particularly important in the Pacific Northwest near the coast (Harmon et al. 1986) where mortality rates of 2.8%/yr have been reported in Sitka spruce forests over a ten year period during gap expansion (Greene et al. 1992, Harcombe et al. 2004). Extremely high levels of wind-caused mortality ($\geq$25%/yr) however are likely rare occurrences. Synoptic wind events operating as "pulse" disturbances have had broad scale and long lasting effects in some parts of the Pacific Northwest near the coast (Sinton et al. 2000), but are generally infrequent and operate at longer time scales than the interval in this study (Sinton and Jones 2002). Increases in chronic wind or synoptic wind events associated with climate change could have large implications for forests through increased mortality, but the effect of climate change on wind disturbance in the Pacific Northwest is poorly understood (Mote et al. 2003).

Although past large-scale studies have implicated fire as an agent of rapid change (e.g. Westerling et al. 2007, Cansler and MacKenzie 2014), most studies are based on remote sensing which are limited to broad severity classes and lack the resolution of pre- and post-fire field-based mortality estimates. Fire appears to be the only natural agent of disturbance resulting in complete stand replacement ($\geq$25%/yr) over short intervals, indicating its potential for causing rapid ecological change and the unique contribution to biodiversity through the creation of diverse early successional habitat. The infrequent occurrence of stand-replacing levels of mortality during the study period (<2% of all rates) at least partially explains the overall rarity of diverse early successional habitat across the region (This dissertation, Chapter 2). Recent increases in the extent and frequency of wildfires have prompted much concern, but there is still a large degree of uncertainty as to the prevalence and effects of high-severity fire. Recent evidence suggests that fire has the potential to restore historic stand structure in some forests where fires have been excluded (Larson et al. 2013), but there is little field-based evidence to indicating how generalizable these results are to a variety of vegetation types. Although tree mortality rates (≥25%/yr) made up approximately a third of all mortality rates in plots with fire, the majority of fire has been non-stand replacing and occurred across a range of low and intermediate levels.

Distribution of mortality rates by vegetation zone

Differences in the cumulative frequency distributions of tree mortality rates among almost all vegetation zones reflect differences in disturbance regimes as well as in the climate and environment that characterize them. The distributions of mortality in the relatively wet western hemlock and silver fir vegetation zones did not differ and are apparently driven primarily by high levels of competition and endemic levels of pathogens. The distribution of mortality rates in cold mountain hemlock and subalpine forests also seems to be driven by high levels of competition and pathogens, but insects and fire played a much larger role. Mortality rates in undisturbed plots were lowest in dry forests, but occurred across all levels as a result of insects and fire in grand fir, Douglas-fir, and ponderosa pine forests.

The distribution of mortality rates in western hemlock and silver fir suggests that mortality generally operates continuously at low levels consistent with the concept of background mortality. Mortality is most likely driven by density dependence in undisturbed plots, which results in frequent mortality events at smaller scales, thus the small proportion of plots with no mortality at all. Small scale endemic infestations of pathogens and disease (Franklin et al. 1987) can elevate mortality for brief periods, but never reached epidemic levels during the study period and rates in plots with pathogens were generally distributed similarly to rates in undisturbed plots. High and extremely high rates of mortality were rare during the study interval, but may be more common during periods of high severity fire (Weisburg and Swanson 2003). Although fire regimes in western hemlock and silver fir are traditionally considered to be characterized by infrequent, stand-replacing fire (Agee 1993), there is increasing evidence that non-stand replacing fire played a much larger role historically (Morrison and Swanson 1990, Weisburg 2004, Tepley et al. 2013). Only a small proportion of the plots in these vegetation zones burned, and mortality rates were limited to levels of mortality levels 1.75-10%/yr suggesting that contemporary fires in wet forests still have mixed-severity effects that may not be that different from historical fires.

The distributions of mortality in cold mountain hemlock and subalpine vegetation zones were similar at lower levels and resembled those of lower elevation wet forests, but subalpine forests had considerably higher levels of mortality (>2.5%/yr) as a result of insects and fire. Pathogens, particularly laminated root rot (*Phellinus weirii*), play an important role in mortality in mountain hemlock but operate primarily at small scales (Hansen and Goheen 2000). Patches of die-back may occur, but require longer time periods to develop due to slow rates of expansion (Matson and Waring 1984). In subalpine forests, the low end of the distribution of mortality rates (particularly the small proportion of plots with no mortality) suggests that background mortality may operate continuously as in wet forests. Earlier snow melt and warmer temperatures under predicted climate change may increase productivity in subalpine forests (Peterson et al.

2002, Nakawatase and Peterson 2006) and increase the role of density dependent mortality, but large proportions of plots at the high levels of mortality from insects and fire indicate that disturbance has been a more prominent driver of change in subalpine forests. Insect outbreaks are part of the historical disturbance regime in many subalpine forests (Smith et al. 2012), but the occurrence of drought has the potential to prolong these (Bigler et al. 2007) and increase cumulative mortality. Approximately 30% of all plots in subalpine forests had stand-replacing mortality levels ($\geq$25%/yr) from fire, the highest of any vegetation zone. These findings corroborate that fires have been especially active in subalpine forest, particularly in the North Cascades of Washington where individual large fires associated with warmer drier climatic conditions have burned with high proportions of high severity fire (Cansler and MacKenzie 2014).

In the absence of disturbance, mortality rates in dry forests of the Pacific Northwest can be low even during a period of extreme drought and dry forests consistently had higher proportions of plots with no mortality detected at all compared to wet or cold forests. As opposed to the continuous background mortality operating in wet forests, mortality in dry forests appears to be more episodic, likely varying over longer time scales with periods of little or no mortality followed by periods with elevated mortality during drought (Villalba and Veblen 1998) that may be the result of insects and fire. There is little empirical data on the actual distributions of mortality in dry forests during drought, but there is some evidence to suggest that a continuum of rates commonly occurs (Elliott and Swank 1994, Allen and Breashears 1998, Mueller et al. 2005). Even in fires, mortality rates occurred across a wide range of mortality levels, again indicating that most fire is predominantly low and moderate severity despite decades of fire exclusion. During the driest 12 year period since 1950 in the southwestern United States, Ganey and Vojta (2011) report median mortality rates of 2%/yr (range=0-28.5%/yr) in unburned mixed conifer forests and 0.4% (range=0-13.6%/yr) in unburned ponderosa pine forests associated with insects. These rates fall within the range found in unburned dry forests during the same period in this study and are consistent with lower mortality in the drier ponderosa pine and higher in the moister grand/white fir and Douglas-fir. Previous studies report that drought related mortality is greatest at the drier end of the moisture gradient (Condit et al. 2004, Allen et al. 2010, Carnicier et al. 2011, Williams et al. 2010, Martinez-Vilalta et a. 2013), but the lowest levels of mortality across the entire region in unburned forests occurred in the hottest, driest vegetation zone, ponderosa pine. These finding indicate that the response of vegetation to climate change is a complex problem and understanding multiple factors may be necessary to predict where changes will occur (Martinez-Vilalta et al. 2013).

Distribution of mortality rates by developmental stage

Mortality rates in early and mid developmental stages in all vegetation zones were mostly <1%/yr. These are low compared to those found in previous studies in temperate and tropical forests (Bible 2001, Chazdon et al. 2005, Lutz and Halpern 2006) which range from to 2- 5%/yr. Some of this difference may be due to the fact that most mortality during early development occurs in smaller size classes not included in this analysis (<7.2 cm dbh). However, this study includes a variety of vegetation zones where multiple pathways of early structural development may occur in addition to rapid establishment and attainment of canopy closure. Most forests in early and mid developmental stages on USFS lands established following logging in the mid to late 20th century (This dissertation, Chapter 2) where density was frequently managed with planting or pre-commercial thinning, specifically with the goals of reducing losses to mortality (Tappenier et al. 2007). Other forests in early developmental stages across the region, particularly in dry and cold vegetation zones, have more likely developed at low density and over longer periods of time (This dissertation, Chapter 2). Density dependent mortality evidently plays less of a role in vegetation zones where forests have been managed or where protracted establishment is a common pathway of early structural development.

Mortality rates in later developmental stages are generally thought to stabilize at lower levels as mortality shifts from density dependent mortality to that associated with the occurrence of pathogens and insects (Franklin et al. 2002). This appears to be the case in western hemlock and silver fir zones where distributions of tree mortality rates shift from 1-2.5%/yr in mature and late stages back towards rates of approximately 1% in undisturbed old-growth plots. These rates are similar to those reported by van Mangtem et al. (2009), but rates in late and old-growth developmental stages of some other vegetation zones were far higher. In less productive vegetation zones including ponderosa pine, Douglas-fir, grand fir/white fir, and subalpine forests where mortality is likely more episodic, rates were far more evenly distributed with relatively large proportions of mortality occurring at higher levels from insects and fire. In dry vegetation zones much of the forest in late and old-growth developmental stages currently exists in denser structural states than they did historically (This dissertation, Chapter 2) and which are thought to be especially vulnerable to disease, insects, and fire (Youngblood et al. 2004). Stand-replacing mortality in a third of forests in late and old-growth developmental stages in ponderosa pine and Douglas-fir, and as much as a half of grand fir/white fir substantiate these concerns, but a valid comparison of historical proportions of high severity fire against current mortality rates is difficult. Historic fire was primarily low severity in the ponderosa pine vegetation zone but mixed severity fires were more common historically in Douglas-fir and grand fir/white fir (Agee 1993).

Trajectories of structural change in Pacific Northwest forests

The framework presented in this study (Fig. 3.1) is intended to enhance understanding of the potential ecological effects of tree mortality in the context of structural development-based directional change in tree density and size. An increase in density and decrease in tree size in densifying forests may indicate vertical and horizontal stratification in canopy gaps or recent periods of recruitment in woodlands. Aggrading forests with increases in tree size and density are indicative of biomass accumulation through tree growth. Thinning forests with decreases in density and increases in tree size may be associated with mortality from density competition or low severity fire that preferentially kills small trees. Die-back indicates decreased tree size from top down mortality of bigger trees and decreased density from lack of recruitment. All four trajectories occurred at levels of mortality up to 2.5%/yr, demonstrating the variety of potential pathways of structural development at relatively low levels of mortality. Thinning was by far the most prevalent trajectory at intermediate levels, but multiple trajectories also occurred at very high levels of mortality ($\geq$25%/yr) where thinning and die-back were the result of fires.

Aggrading stands were primarily limited to levels of mortality <2.5%/yr. This developmental trajectory occurred during all stages of development, but was far more prevalent in early stages and decreased rapidly during later developmental stages in all vegetation zones. Increases in density and mean tree size suggest that stands with this trajectory have some the highest rates of growth similar to previously described developmental phases including biomass accumulation (Franklin et al. 2002) and aggradation phases (Bormann and Likens 1979). Despite extreme drought conditions during the study period (Schwalm et al. 2013) and evidence that younger forests may be more sensitive to drought (Luo and Chen 2013), the prevalence of the aggrading trajectory and relatively low mortality rates indicate that forests in early developmental stages maintained positive levels of biomass accumulation. Although growth may be decreased during drought conditions, survival of larger more dominant trees will increase chances of developing characteristics of later developmental stages in the future.

Stands going through densification were also primarily limited to levels of mortality <2.5%/yr. An increase in density and corresponding decrease in tree size suggests that recruitment is the dominant process driving this trajectory. Although this trajectory occurred in most stages of development in all vegetation zones, it rarely made up more than 30% of any specific stage in any vegetation zone. Densification in earlier developmental stages may occur following pulses of recruitment when establishment is protracted. In later developmental stages it may be indicative of understory re-initiation

(Oliver and Larson 1990) and vertical diversification (Franklin et al. 2002) following single or multiple tree gaps that are rapidly filled with recruitment of advanced regeneration as the result of windthrow or senescence of old trees (Lertzman 1992). However, densification is also often associated with the cessation of frequent low severity disturbances such as fire (Goforth and Minnich 2008, Raumann and Cablk 2008, Hanberry et al. 2014) or seasonal flooding (Conner et al. 1981, Johnson and Waller 2013) as well as changes in land use practices (Vila-Cabrera et al. 2011). Densification was likely more common in dry woodland forests of the Pacific Northwest and other parts of the western United States during the 20th century than during this study period as a result as a result of fire exclusion, grazing, and high grade logging (Youngblood et al. 2004, Merschel et al. 2014, Goforth and Minnich 2008, Powell et al. 2013, Dolanc et al. 2014). Given increase in wildfire extent and severe drought during the study period, it is surprising that this type of structural development is still occurring in some dry forests in the Pacific Northwest, particularly in later developmental stages where it makes up from approximately 10-12% of late and old-growth developmental stages in ponderosa pine and Douglas-fir, and 20% of grand fir/white fir.

Thinning occurred across the widest range of mortality levels and was by far the most common trajectory of structural change in all vegetation zones. Decreases in density and increases in tree size are the result of differential mortality by size. Asymmetric competition between trees of different sizes (Peet and Christensen 1987) results in diameter differentiation (Oliver and Larson 1990) and dominance of larger more competitive trees in undisturbed forests. Thinning is primarily associated with earlier developmental stages such as stem exclusion (Oliver and Larson 1990, Lutz and Halpern 2006) where it plays an important role through maturation (Franklin et al. 2002). However, the prevalence of thinning increased consistently in later developmental stages in all vegetation zones. Although recent studies have demonstrated the importance of density dependent mortality at low mortality rates in old-growth forests (Lutz et al. 2014), disturbance agents are more likely the driver of the thinning trajectory at mortality levels >1%/yr. Evidently, most mortality associated with disturbance operates from the bottom up where smaller trees are subject to higher mortality than larger trees at higher rates. This pattern has been observed in forests as a result of drought (Lloret et al. 2004), but is common with insects and especially with fire where larger trees have thicker bark that insulates and protects the cambium (Harmon 1984) and higher canopies that can reduce crown scorch. At high levels of mortality up to 25%/yr, thinning appears to accelerate structural development by increasing the dominance of larger trees, thus potentially increasing resistance to future drought (Waring and Pitman 1985)

Stands exhibiting die-back with a decrease in both density and tree size were by far the least common trajectory of structural change in all vegetation zones and all developmental stages. It occurred across all levels of mortality, but only made up a large portion of plots with stand-replacing mortality levels (≥25%/yr). It was most common in later developmental stages where it results from top-down mortality and loss of a single or group of canopy trees (Mueller-Dombois 1987) with little short term subsequent recruitment. This may occur gradually at low mortality rates in some vegetation zones during gap phase dynamics or as early successional cohorts age and senescence (Ward

1982, Franklin et al. 2002). Die-back may occur at higher levels of mortality over short intervals during insect outbreaks where it can accelerate successional turnover by rapidly eliminating an early successional species (Veblen 1991). Die-back makes up approximately half of all mortality rates ≥25%/yr where it is strictly associated with stand-replacing fire. This has resulted in the rapid initiation of early stand development in productive vegetation zones (Larson and Franklin 2005, Brown et al. 2013), but may take longer take much longer in dry or cold vegetation where recruitment might be limited by competition from shrubs or herbaceous vegetation (Riginos 2009), climate (Brown and Wu 2005), dispersal limitation (Agee and Smith 1984), or a combination of these factors (Acacio et al. 2007).

Effects of Mortality on Regional Forest Change

Differences in the distributions of mortality rates among vegetation zones and developmental stages indicate that the rate and extent of structural change associated with tree mortality varied widely across the region during the study period. Past studies have suggested that the effects of mortality associated with drought may be greatest in the driest forests (Condit et al. 2004, Allen et al. 2010, Carnicier et al. 2011, Williams et al. 2010, Martinez-Vilalta et a. 2013), but I found that the hottest driest vegetation zone, ponderosa pine, had some of the lowest levels of mortality in the Pacific Northwest. Differences in mortality among vegetation zones may be related to productivity and disturbance, but legacies of past disturbance and management that determine state and abundance of forests in various stages of structural development are also important factors affecting regional forest dynamics in the Pacific Northwest.

Wet forests had the least amount of change as a result of mortality during the study period and structural change was largely a product of growth (Whittier and Gray 2014). The limited extent of wildfire and predominantly endemic levels of insects and pathogens in these vegetation zones during the study period suggest that stand-level processes were the primary drivers of recent dynamics. Low levels of mortality in early and mid developmental stages were unexpected given rates reported in past studies (Bible 2001, Lutz and Halpern 2006, but are likely the result of past thinning. However, mortality rates in old-growth forests correspond with rates observed in other studies of mortality in old-growth forests of the region during the same time period (van Mantgem et al. 2009) that found higher levels of mortality than in the 1970's and 80's. If the short term trajectories observed here continue, there could be long term changes in structure of old-growth forest in wet vegetation zones. The prevalence of thinning in later developmental stages strongly suggests that although the big tree component may remain, these forests may be less dense if they continue on this trajectory of structural change.

Considerable differences in the distribution of mortality rates between mountain hemlock and subalpine vegetation zones indicate differences in the extent and magnitude of recent change in cold forests. Mountain hemlock forests were more similar to wet vegetation zones and most structural change in the absence of disturbance may be subtle and manifest itself over longer time scales as the result of elevated rates of background mortality. Subalpine forests, however, experienced some of the greatest change observed in any vegetation zone during the study period. Insects and especially wildfires have affected large extents and resulted in considerable mortality in late and old-growth developmental stages. In subalpine forests where structural development is extremely slow even under historical climatic conditions (This dissertation, Chapter 2), recent mortality has likely caused some of the longest lasting effects in the entire region.

Dry forests also had some of the highest levels of mortality during the study period, but exhibited considerable variation among vegetation zones. Surprisingly, many ponderosa pine forests had little to no mortality in the absence of insects or fire. Instead, the more productive higher elevation Douglas-fir and grand fir vegetation zones had some of the highest levels of mortality of all vegetation zones, particularly in late and old-growth developmental stages where the legacy of fire suppression is evident in all dry vegetation zones (This dissertation, Chapter 2). However, most of this mortality, even at levels up to 25%/yr, is associated with thinning from fire and insects. The observed decreases in density and increases in the dominance of bigger trees may be restoring some aspects of historical structure and potentially increasing resilience to future wildfires and drought, but further analysis on compositional change is needed. Although forests in later developmental stages have experienced some stand replacing fire in dry vegetation zones, the extent of that is still densifying forests is far greater. Even during a period with the greatest drought and most widespread fire since the early 1900's, losses to mortality from stand replacing fire were far exceeded by growth and recruitment in densifying forests.

Conclusions

This study offers the first regional scale investigation of variation in short interval mortality rates from all sources across multiple vegetation zones. Most rates were within those reported by other studies of background mortality and stand replacing rates were rare, but over 30% of the plots had rates in between 1%/yr and 25%/yr from pathogens, insects, and fire. Recognizing that a broad continuum of mortality rates occurs as the result of low and moderate severity disturbances, as well as the differences in the time scales over which they operate, is necessary to fully understand dynamics at a regional scale. Pulse disturbances such as fire may result in rapid change from higher levels of mortality across large extents, but press disturbances such as insects affect much greater extents at lower rates. Comparing the effects of these disturbances may thus depend on duration as much as on short term mortality rates.

Differences in the distribution of mortality rates among vegetation zones in the Pacific Northwest indicate that not all forests are responding the same way to the recent changes in climate and disturbance regimes. Changes in forests with disturbance regimes including more frequent fire and insect activity like subalpine and dry forests of the region will occur more rapidly with more obvious ecological effects. Changes may be more subtle in other forests such as western hemlock, silver fir, and mountain hemlock. In the absence of disturbance, small changes in demographic rates will manifest themselves over longer time scales.

Few if any generalizations regarding differences in mortality in forests of different developmental stages could be made. I found little evidence to support the hypothesis that forests in early stages of development exhibit higher mortality than those in later stages, but this may be because most forests in early developmental stages in the region have either been managed or developed at low densities. Mortality rates in old-growth forests of wet vegetation zones were similar to those reported by van Mantgem et al. (2009), indicating the potential for change in the structure and function of these over longer time scales from decreased density and biomass of live trees. However, rates occurred at much higher levels in late and old-growth developmental stages in subalpine and dry vegetation zones as a result of disturbance. In dry vegetation zones this is likely associated with fire suppression and past management which has altered structure with increased density.

Application of a simple framework characterizing trajectories of structural change offered important new insights into the effects of mortality in different forests. Most forests in the region appear to be going through a period of thinning following a trajectory of decreased density and increased tree size. Even at very high rates of mortality this trajectory may have ecological benefit, particularly in dry forests which are presently dominated by high density forests (This dissertation, Chapter 2). However, it is apparent that even during a period of drought and widespread wildfire, growth may exceed mortality as the occurrence of densification in dry forests was far greater than thinning at high levels of mortality. Die-back was rare, particularly at mortality rates high enough to result in stand replacing mortality, substantiating the overall rarity of diverse forests in early developmental stages around the region. However, if 2 % of a vegetation zone is subject to mortality rates at stand replacement levels every 8 years, we can expect large changes in forests over the next century, especially in less productive forests, where growth and recruitment are slow.

The large degree of variation in mortality rates and subsequent effects on stand structure indicate that predicting the effects of future change in climate and disturbance will have on forested ecosystems will require far more than just examining mortality rates or focusing on change associated with disturbance alone. Future changes in ecosystem structure and function are likely to manifest themselves at different rates and through a variety of mechanisms including subtle changes in demographic rates and rapid change associated with disturbance. Incorporating variation in structural change can vastly improve our understanding of how mortality will affect future ecosystem function. Although some structural change associated with higher levels of mortality in dry forests may increase resilience to future fire and drought, structural changes associated with decreased density in wet forests may affect potential to store carbon or function as wildlife habitat. A short term look at mortality rates across a region offers much in terms of insights into the how the potential for change may vary across the region, but it is just a snapshot and there is still much uncertainty in how forests will change in the future. More work is needed to address the stability of mortality rate distributions over time to advance our conceptual understanding beyond background mortality, especially in dry forests where mortality may be more episodic. Likewise, further work on size and species-specific mortality rates would greatly inform our understanding of compositional/successional changes in the context of resilience to future fire and drought. Finally, an investigation of specific drivers of mortality and their interactions (e.g. drought, density dependence) is needed to provide a mechanistic understanding of how forest may change under future climate and disturbance scenarios.

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Tables and Figures

Table 3.1. Proportion of each vegetation zone classified into one of four trajectories of structural change by developmental stage based on the following criteria: “densifying”= $\Delta TPH \geq 0$ and $\Delta QMD < 0$, “aggrading”= $\Delta TPH \geq 0$ and $\Delta QMD \geq 0$, “die-back”= $\Delta TPH < 0$ and $\Delta QMD < 0$, and “thinning”= $\Delta TPH < 0$ and $\Delta QMD > 0$.

	Densifying	Aggrading	Thinning	Die-back
All	0.18	0.19	0.58	0.05
Western Hemlock	0.12	0.16	0.69	0.02
Early	0.00	0.69	0.31	0.00
Mid	0.14	0.30	0.54	0.02
Mature	0.11	0.16	0.70	0.03
Late	0.10	0.08	0.80	0.02
Old-Growth	0.16	0.08	0.74	0.02
Silver Fir	0.20	0.19	0.57	0.04
Early	0.00	0.87	0.13	0.00
Mid	0.11	0.62	0.27	0.00
Mature	0.19	0.18	0.56	0.07
Late	0.20	0.08	0.69	0.03
Old-Growth	0.30	0.06	0.56	0.08
Mountain Hemlock	0.23	0.15	0.56	0.06
Early	0.08	0.58	0.33	0.00
Mid	0.23	0.28	0.50	0.00
Mature	0.27	0.34	0.36	0.03
Late	0.00	0.08	0.92	0.00
Old-Growth	0.23	0.10	0.60	0.07
Subalpine	0.18	0.15	0.59	0.08
Early	0.48	0.52	0.00	0.00
Mid	0.32	0.22	0.42	0.04
Mature	0.16	0.28	0.48	0.09
Late	0.10	0.01	0.72	0.17
Old-Growth	0.17	0.08	0.67	0.08
Grand/White Fir	0.24	0.17	0.54	0.05
Early	0.15	0.67	0.19	0.00
Mid	0.26	0.27	0.42	0.05
Mature	0.30	0.26	0.41	0.02
Late	0.20	0.16	0.60	0.04
Old-Growth	0.23	0.09	0.62	0.06
Douglas-fir	0.13	0.21	0.60	0.06
Early	0.00	0.76	0.14	0.10
Mid	0.14	0.25	0.54	0.06
Mature	0.16	0.22	0.58	0.03
Late	0.15	0.19	0.50	0.15
Old-Growth	0.11	0.14	0.70	0.05
Ponderosa Pine	0.15	0.34	0.48	0.03
Early	0.04	0.43	0.52	0.00
Mid	0.18	0.43	0.38	0.02
Mature	0.15	0.39	0.44	0.02
Late	0.10	0.13	0.68	0.09
Old-Growth	0.18	0.12	0.64	0.06

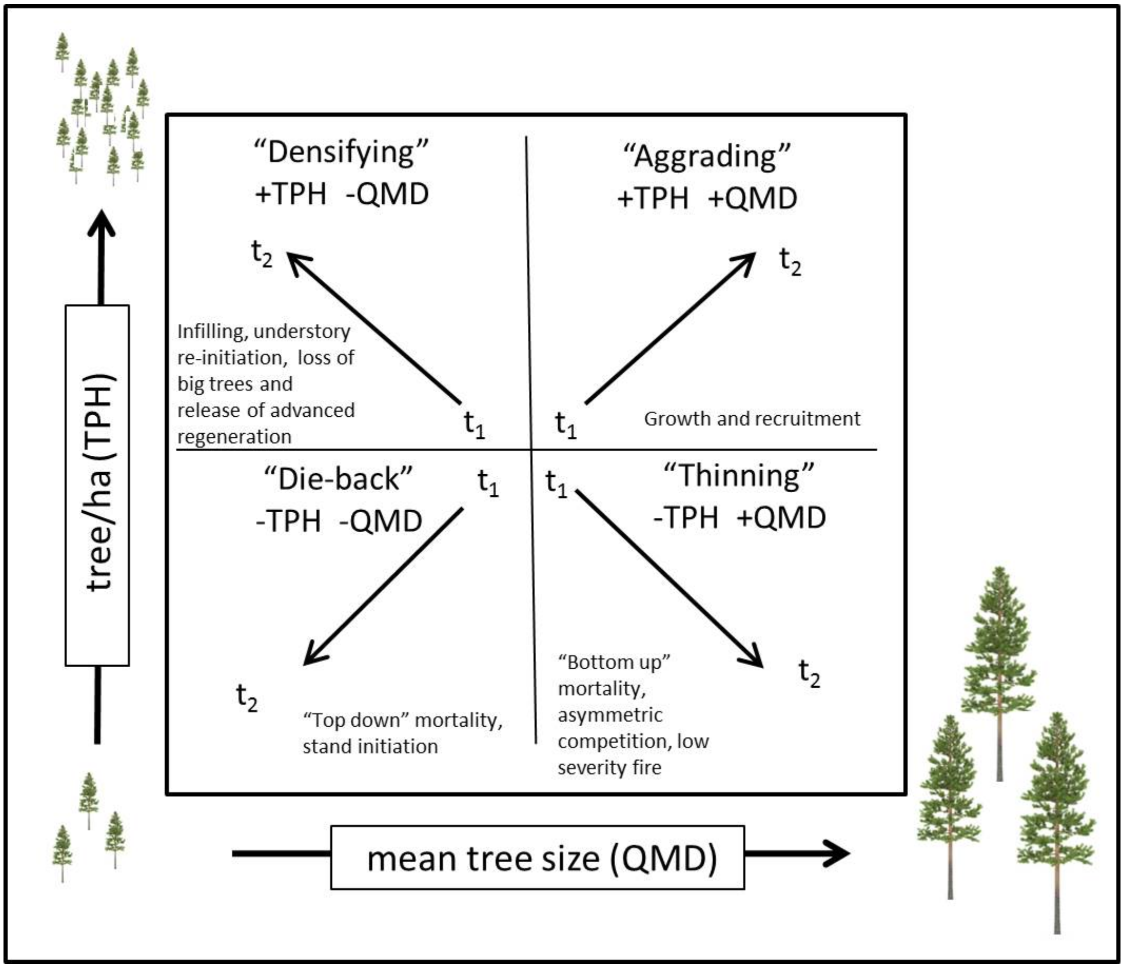

Figure 3.1. Four trajectories of structural development based on changes in the density of live trees per ha (TPH) and quadratic mean diameter (QMD) and associated developmental processes expanded from Coomes and Allen (2007). In a)"densifying": ΔTPH$\geq$0 and ΔQMD <0, b) "aggrading": ΔTPH $\geq$0 and ΔQMD $\geq$0, c) "die-back": ΔTPH <0 and ΔQMD <0, and d)"thinning": ΔTPH<0 and ΔQMD>0.

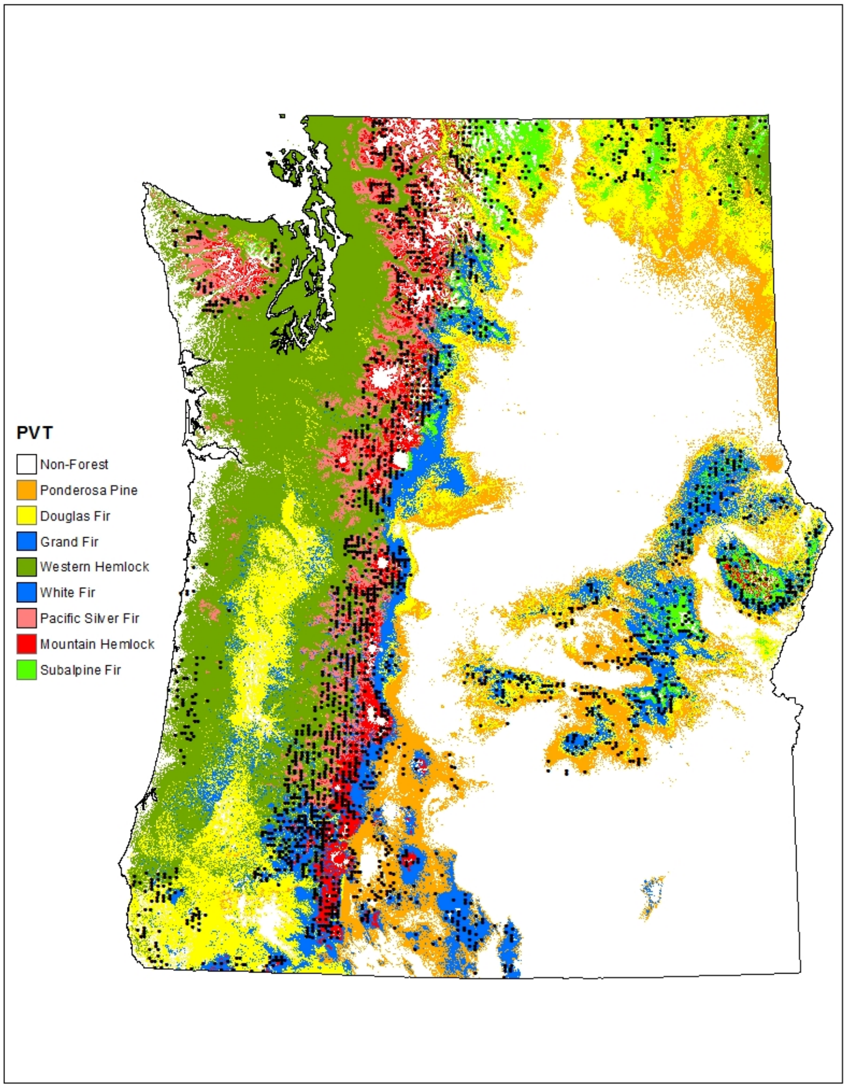

Figure 3.2. Major potential vegetation zones of the Pacific Northwest following Henderson et al. (2011) and approximate locations of Current Vegetation Survey plots on United States Forest Service lands.

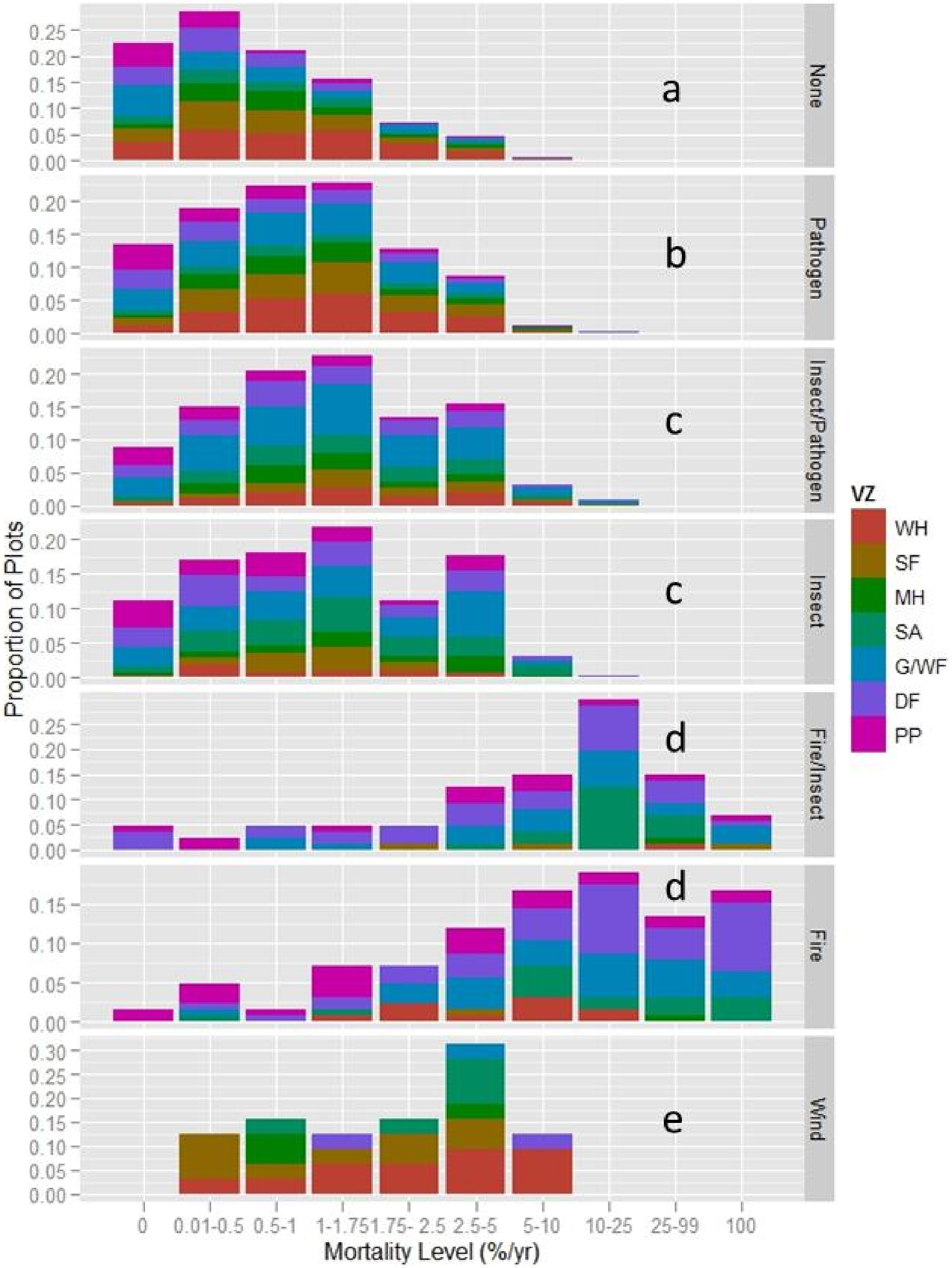

Figure 3.3. Histograms of mortality rates for specific disturbances including none, pathogens, pathogens and insects, insects, insects and fire, fire, and wind. Disturbances that share the same letter do not differ significantly from each other ($p<0.05$) based on a test comparing Wald F-statistics. .

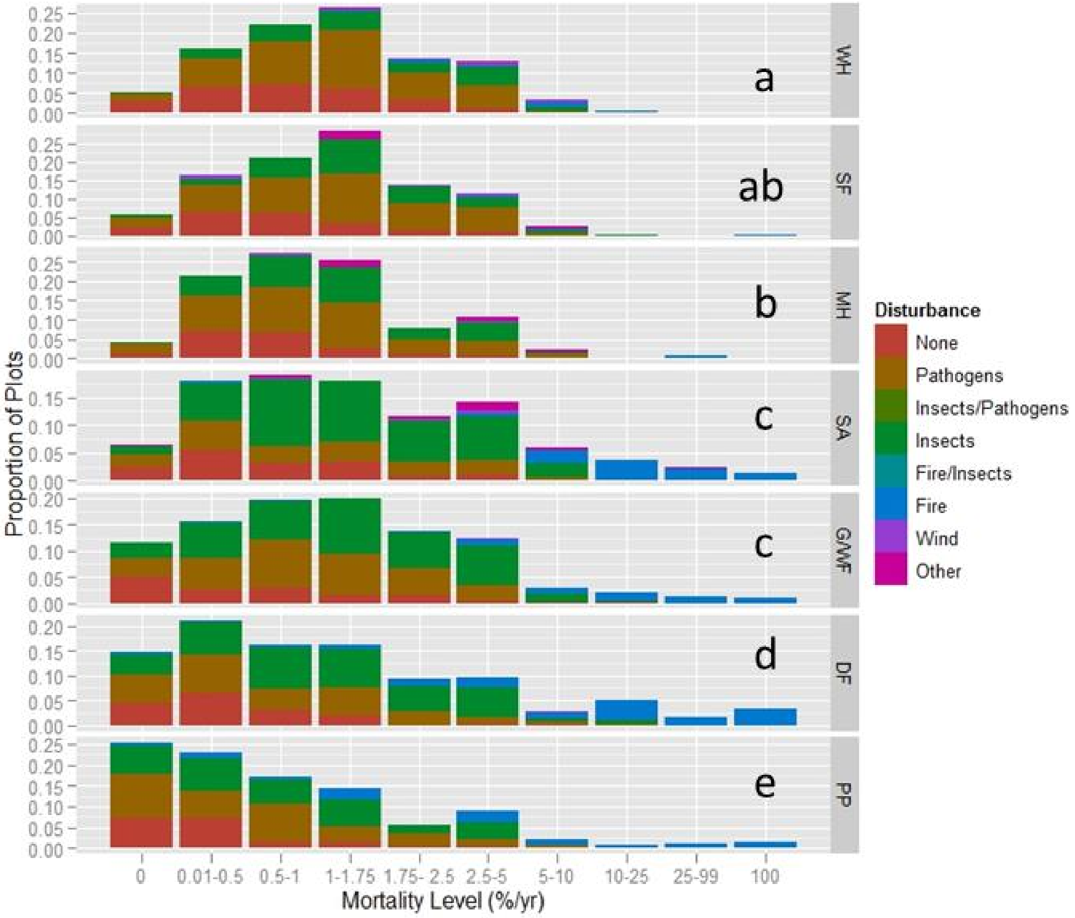

Figure 3.4. Histograms of mortality rates for western hemlock (WH), silver fir (SF), mountain hemlock (MH), subalpine forests (SA), grand fir/white fir (G/WF), Douglas-fir (DF), and ponderosa pine (PP). Vegetation zones that share the same letter do not differ significantly from each other ($p<0.05$) based on a test comparing Wald F-statistics.

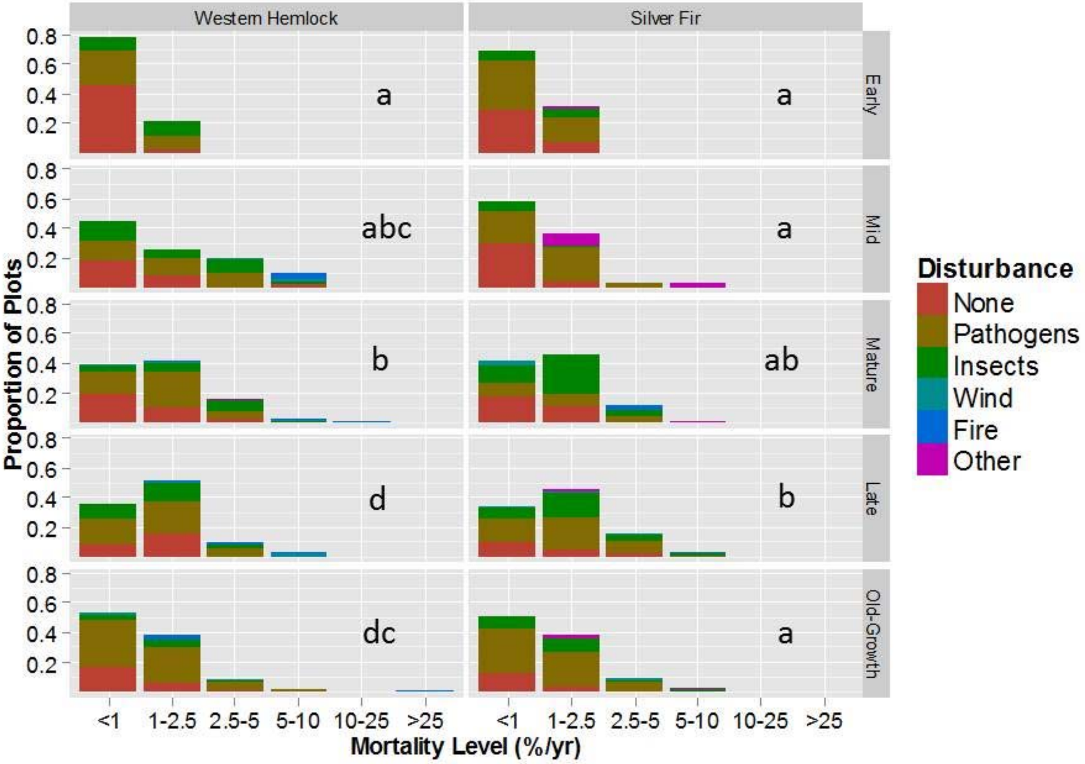

Figure 3.5. Histograms of mortality rates for early, mid, mature, late and old-growth stages of structural development in wet vegetation zones of the Pacific Northwest including western hemlock and silver fir. Developmental stages that share the same letter do not differ significantly from each other ($p<0.05$) based on a test comparing Wald F-statistics.

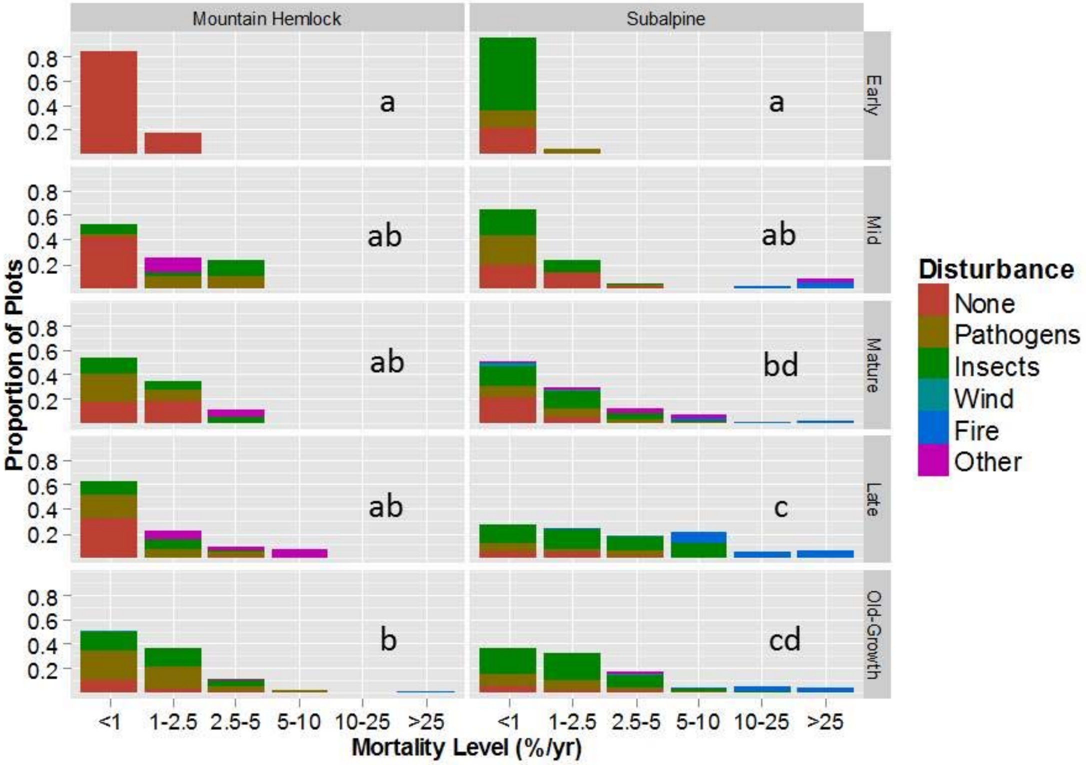

Figure 3.6. Histograms of mortality rates for early, mid, mature, late and old-growth stages of structural development in cold vegetation zones of the Pacific Northwest including mountain hemlock and subalpine fir. Developmental stages that share the same letter do not differ significantly from each other ($p<0.05$) based on a test comparing Wald F-statistics.

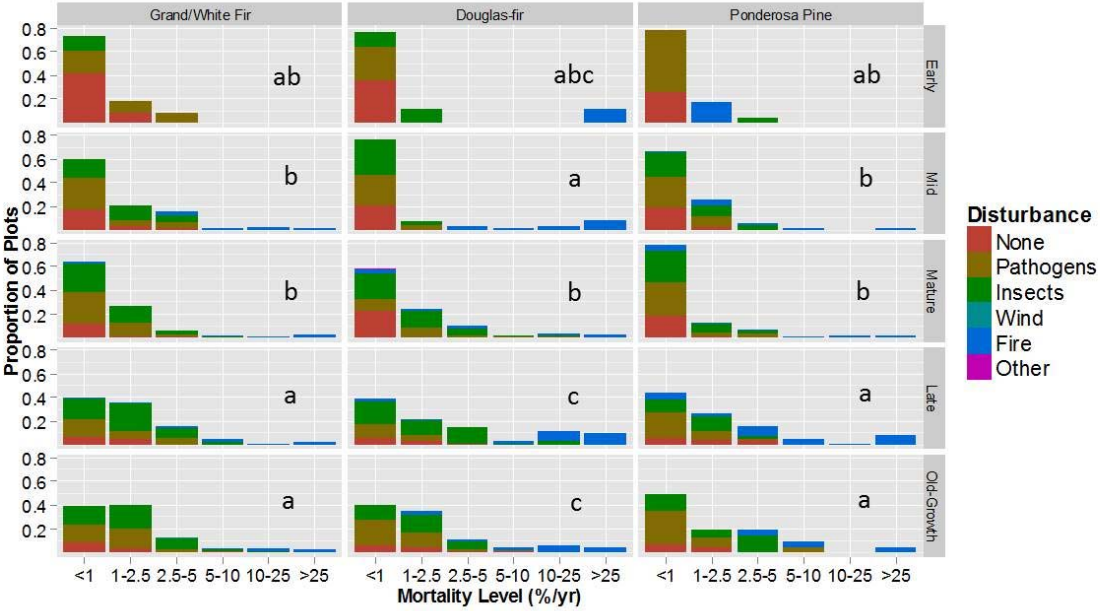

Figure 3.7. Histograms of mortality rates for early, mid, mature, late and old-growth stages of structural development in dry vegetation zones of the Pacific Northwest including grand fir/ white fir, Douglas-fir, and ponderosa pine. Developmental stages that share the same letter do not differ significantly from each other ($p<0.05$) based on a test comparing Wald F-statistics.

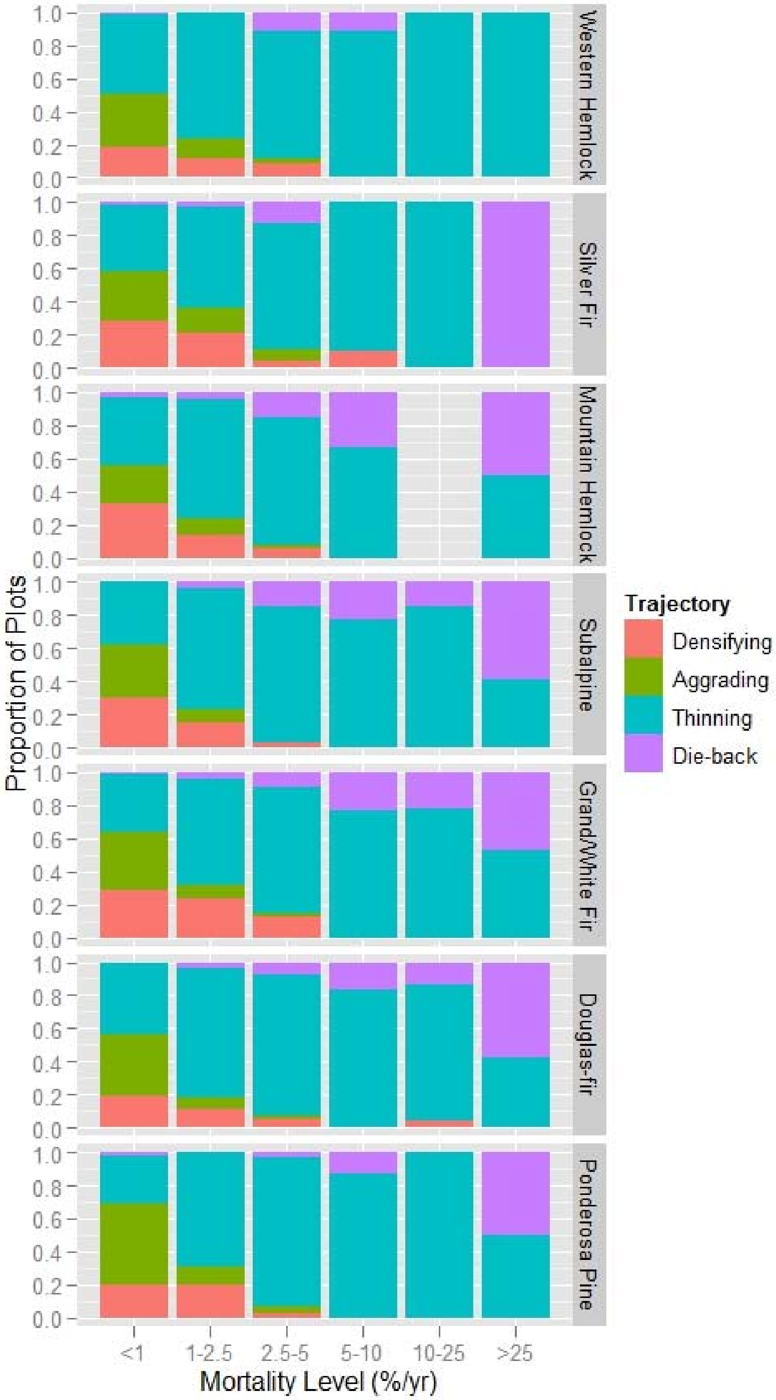

Figure 3.8. Proportion of plots at different levels of tree mortality in each of the major forested vegetation zones of the Pacific Northwest classified into one of four structural trajectories based changes in density of trees per ha and quadratic mean diameter where: "densifying"= ΔTPH≥0 and ΔQMD <0, "aggrading"= ΔTPH ≥0 and ΔQMD ≥0, "thinning"= ΔTPH<0 and ΔQMD>0, and "die-back"= ΔTPH <0 and ΔQMD <0.

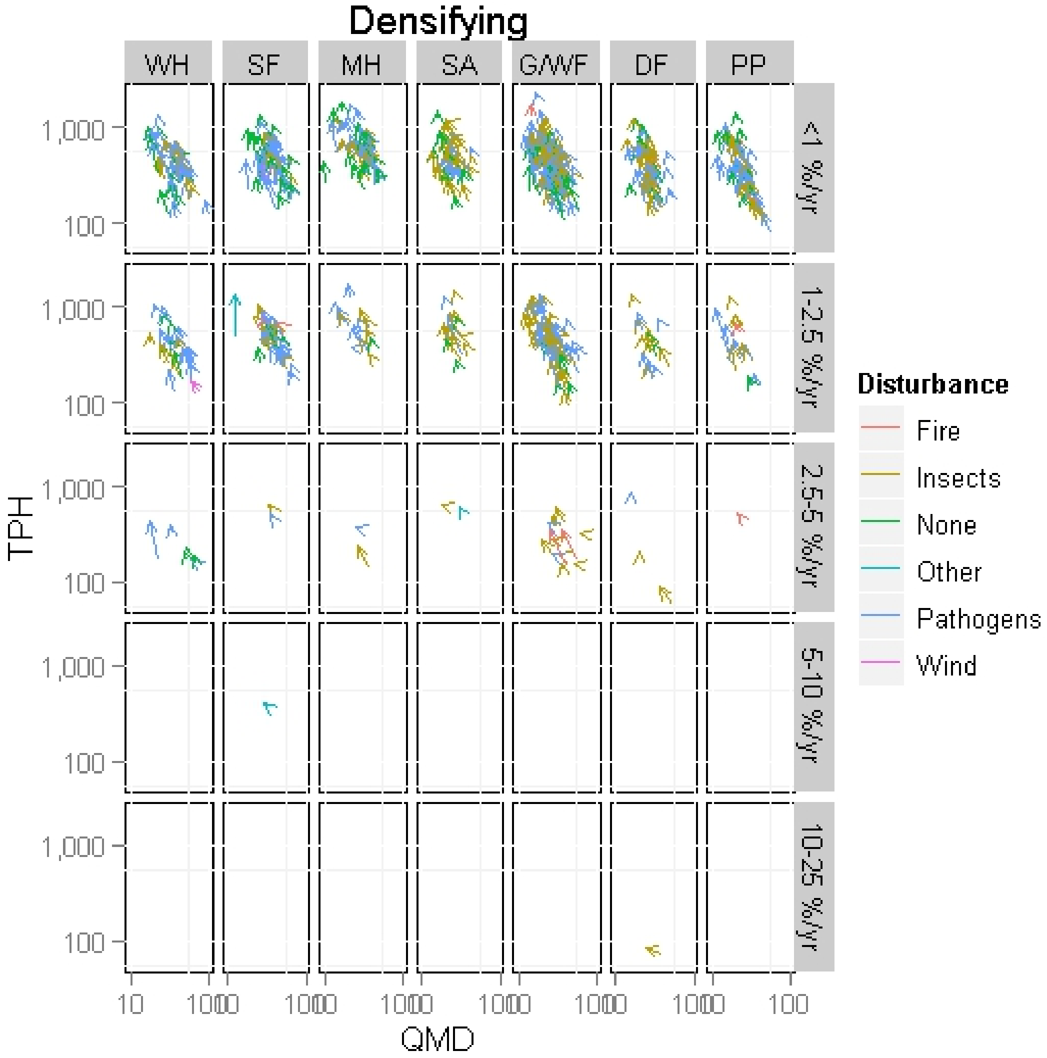

Figure 3.9. Changes in quadratic mean diameter and density of trees per ha for plots classified as “densifying” (ΔTPH≥0 and ΔQMD <0) by mortality level for the major forested vegetation zones of the Pacific Northwest.

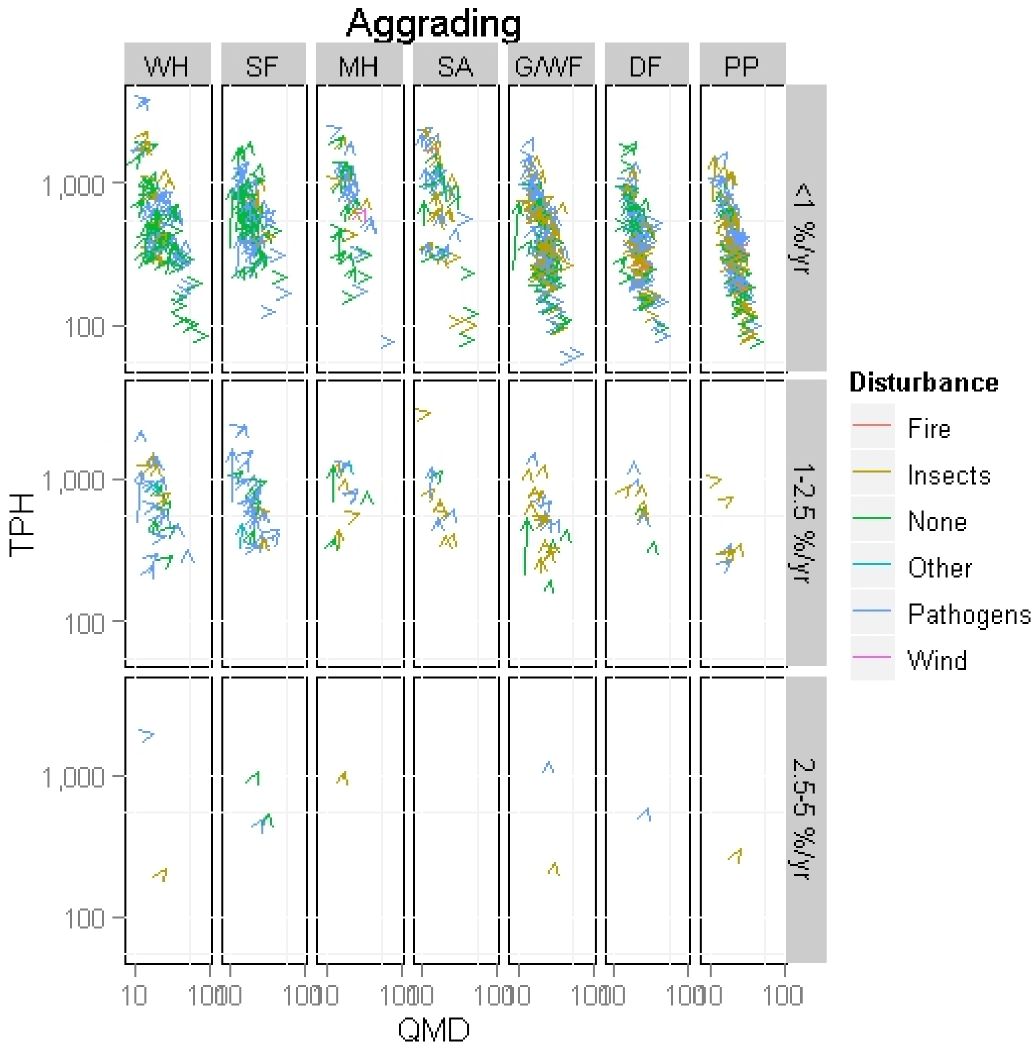

Figure 3.10. Changes in quadratic mean diameter and density of trees per ha for plots classified as "aggrading" (ΔTPH ≥0 and ΔQMD ≥0) by mortality level in the major forested vegetation zones of the Pacific Northwest.

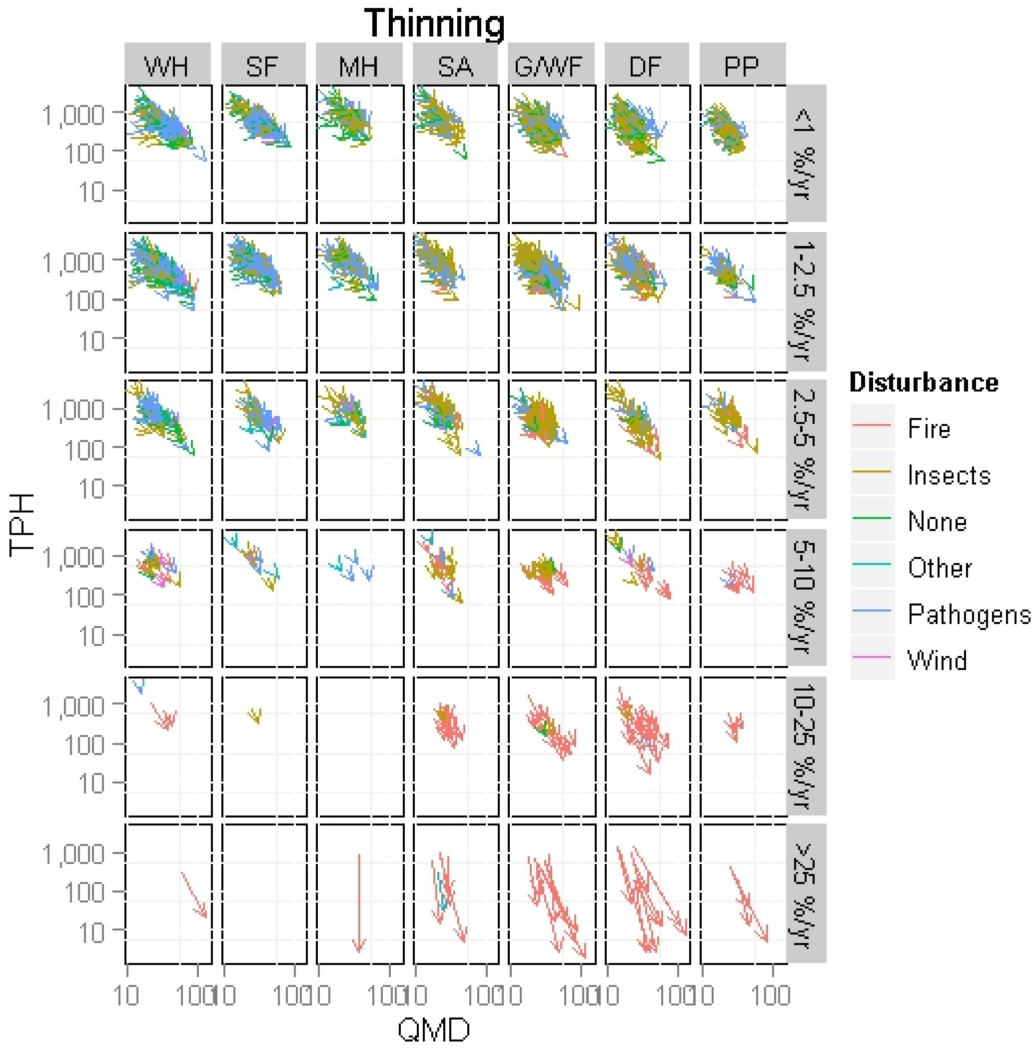

Figure 3.11. Changes in quadratic mean diameter and density of trees per ha for plots classified as "thinning" ($\Delta TPH<0$ and $\Delta QMD>0$) by mortality level in the major forested vegetation zones of the Pacific Northwest.

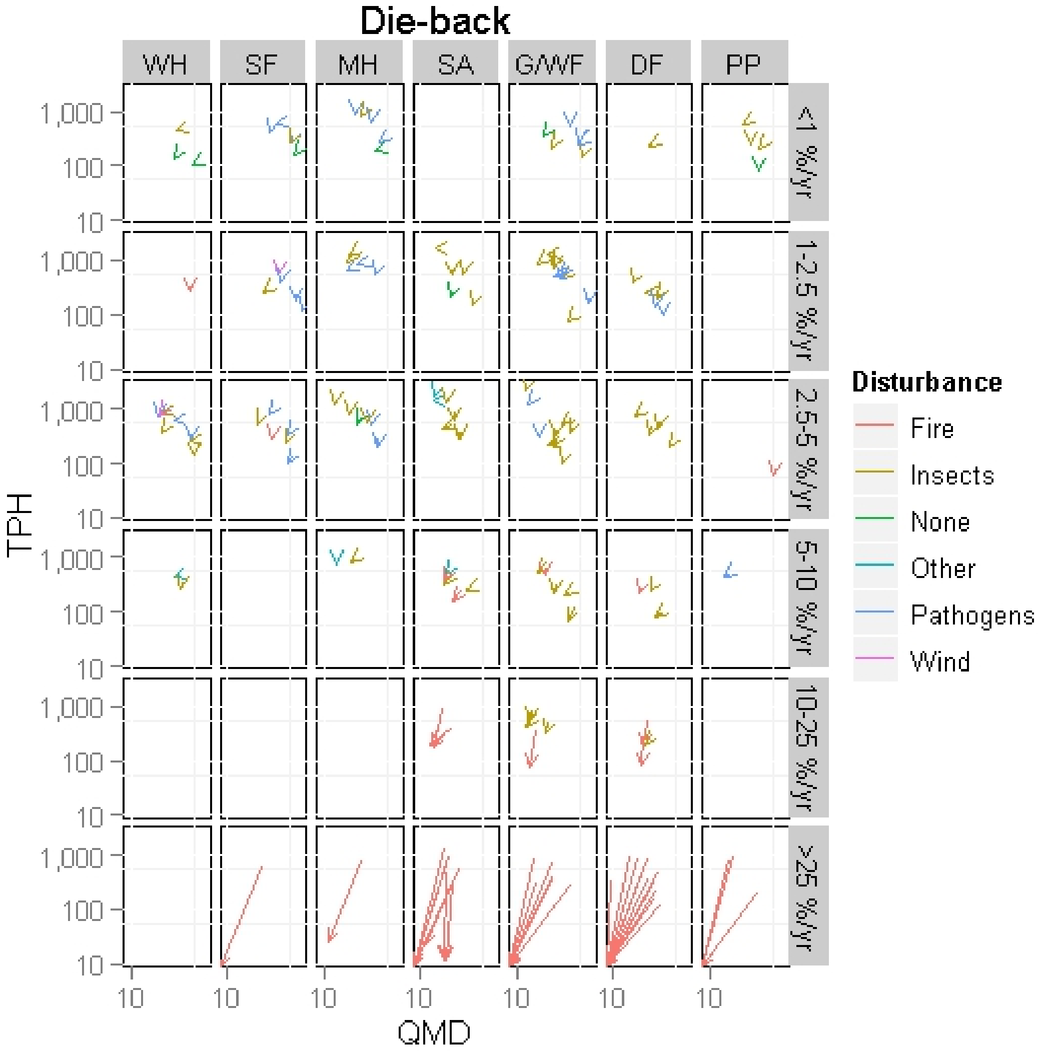

Figure 3.12. Changes in quadratic mean diameter and density of trees per ha for plots classified as “die-back” (ΔTPH <0 and ΔQMD <0) by mortality level in the major vegetation zones of forests of the Pacific Northwest.

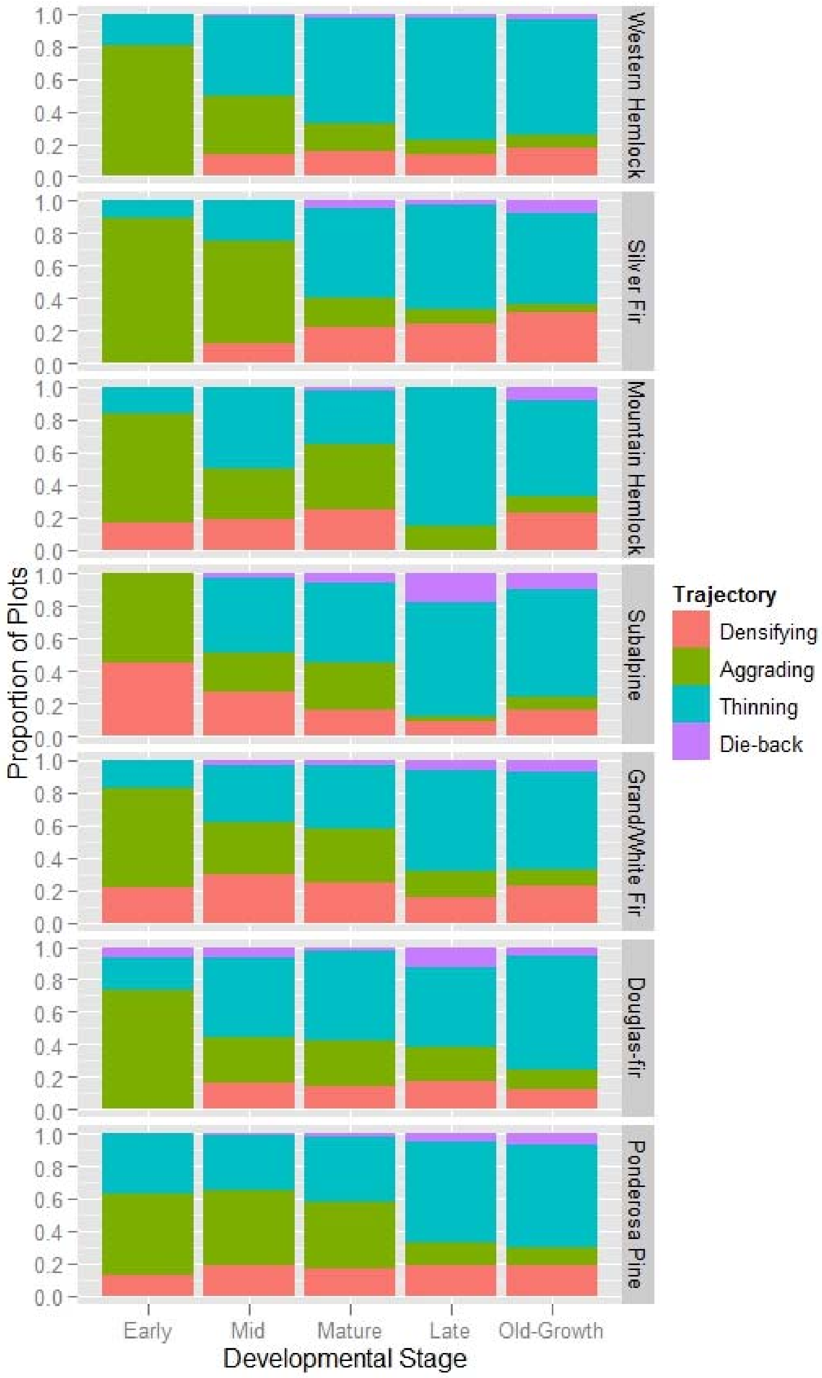

Figure 3.13. Proportion of plots in different stages of structural development in each of the major forested vegetation zones of the Pacific Northwest classified into one of four trajectories of structural change based changes density of trees per ha and quadratic mean diameter where: “densifying”= ΔTPH$\geq$0 and ΔQMD <0, “aggrading”= ΔTPH $\geq$0 and ΔQMD $\geq$0, “thinning”= ΔTPH<0 and ΔQMD>0, and “die-back”= ΔTPH <0 and ΔQMD <0.

Chapter 4: Conclusions and Synthesis

Recent climatic warming trends and increased wildfire occurrence have caused much concern regarding tree mortality and associated changes in forest ecosystems worldwide as well as in the Pacific Northwest. Despite this concern, few empirically-based characterizations of tree mortality and forest dynamics have been conducted for any forest region. Consequently, there has been a large amount of uncertainty regarding cumulative effects of stand-level change on regional dynamics. Much of this uncertainty has been due to limited application of regional field based inventories and oversimplified conceptual models of structural development and the associated effects of tree mortality on structural development. The results of this dissertation offer novel insights that substantially reduce this uncertainty in the Pacific Northwest but also have broader implications for conceptualizing structural development and the effects of tree mortality at stand and regional scales.

The results of this dissertation indicate that the turn of the 21st century brought with it a period of rapid change in some forests of the Pacific Northwest. Large wildfires and insect outbreaks resulted in episodes of tree mortality and rapid change in the structure of many forests, but certainly not all. Even with an increase in the frequency and extent of wildfires, I found that stand-replacing levels of mortality were relatively rare across the region and most mortality associated with disturbance occurred across a range of levels during this time period. The extent of stand-replacing disturbance events was reflected in the overall rarity of forest in early developmental stages, especially compared to that of forests in later developmental stages which still dominated the region. However, differences in levels of mortality among vegetation zones and stages of structural development indicated that the rate and extent of change during this period were highly variable. Thus, the cumulative ecological effects of recent forest dynamics were by no means uniform across the region and varied greatly at smaller spatial scales.

The dynamics during the study interval in unmanaged wet forests on USFS lands were primarily the result of low levels of background mortality. Overall, dynamics of forests in early and mid developmental stages were apparently driven by growth and recruitment with trajectories of structural change toward later developmental stages with bigger trees. Forests in later developmental stages matured developmentally, but along a different trajectory. Increases in density and decreased tree size were likely associated with understory re-initiation and vertical diversification following loss of single or a few canopy trees, but most stands decreased in density and increased in mean tree size from density dependent related mortality of smaller trees. Although mortality rates may be increasing in old-growth forests, it appears that most of the associated structural change resulted from decreased density of smaller trees as opposed to changes in other elements of structure, particularly bigger trees which take longer to develop and are a key element of old-growth structure.

Unmanaged dry forests on USFS lands experienced far greater than change than wetter forests during the study interval. The occurrence of wildfires and ongoing insect outbreaks resulted in a much greater extent and magnitude of structural change than in wet vegetation zones. Similar to wet vegetation zones, most forests in early and mid developmental stages are on trajectories of structural change toward later developmental stages with bigger trees and lower overall density. Likewise, some forests in later developmental stages also matured structurally, but often far more rapidly and across larger spatial extents as a result of relatively high mortality related to disturbance. However, even at higher levels of mortality, most forests in later developmental stages were thinning based on overall decreases in density and increased dominance of bigger trees. In some cases, recent mortality from fires appears to be restoring some aspects of historical forest structure. This outcome was more common than complete stand-replacement in fire, but the extent of both together is still far less than that of the forest that increased in density.

The cumulative effects of recent dynamics in wet forests were minimal and the distribution of forests in various developmental stages is still primarily the legacy of past disturbances, even at the scale of individual vegetation zones. Clearcutting on private lands has maintained the presence of forest in early developmental stages, but structurally diverse types with live and dead legacies from wildfire are extremely rare, even compared to the abundance old-growth forests. In this light, recent fires have increased structural diversity across all spatial scales as most fires have either been small or contained a range of levels of mortality. The cumulative effects of wildfire in dry forests were much greater. Wildfires increased the abundance of early developmental stages, but mortality associated with insects and low and moderate severity fire have also resulted in far more forest in later developmental stages with high densities of snags. Like wet forests, the cumulative effects or recent forest dynamics have increased structural diversity at the scale of individual vegetation zones, but the effects on landscape diversity at smaller scales may differ. Even though most wildfire has been low or moderate in severity, large patches of high severity fire have the potential to reduce the extent of forest in later developmental stages and eliminate big, old trees that may take centuries to redevelop. In this light, increases in structural diversity at larger spatial scales may come as a tradeoff with losses of old-growth at landscape scales and in critical locations where it may be need to support populations of listed species. Quantifying this trade-off and the spatial scales at which they have occurred are an important next step in understanding the effects of recent wildfires.

The empirically-based structural classification offers a novel approach to understanding structural variability across broad geographic extents. Inclusion of the dead wood and understory components of structure as opposed to strictly live tree biomass offer additional insight into ecosystem function in the context of wildlife habitat and biodiversity. Likewise, the emergence of multiple lower density structural types offers new insights into the development of woodlands from non-forested states (e.g. grasslands and shrublands) as well as transition to and from forested states. Application of the structural classification to multi-temporal data in a state-and-transition framework has the potential to document prevalent developmental pathways and validate such an approach for tracking forest dynamics. This application could be done with multi-temporal inventory data, but incorporation of remote sensing also has the additional potential to quantify rates of change and elucidate scale dependent trade-offs related to biodiversity resulting from the occurrence of individual events (e.g. large wildfires). Finally, given the wide range of structural variation present in the Pacific Northwest, the framework could be applied across all of western North America where recent systematic forest inventories exist, but uncertainty still remains regarding the cumulative effects of recently documented mortality.

Examination of a regional scale distribution of short term mortality rates and application of a simple framework characterizing trajectories of structural change offered important new insights into the effects of mortality in forests differing in productivity and disturbance regimes. Most past investigations of tree mortality have either excluded or focused specifically on disturbed forests or a single disturbance type (e.g. fire), but results of this dissertation highlight the need for and value of examining mortality across a range of disturbance types and levels of mortality to understand the cumulative effects at regional scales. Furthermore, most studies of mortality have been conducted in the context of biomass accumulation, but I found that mortality at relatively high levels can result in structural change towards later developmental stages based changes in tree size. These results provide context regarding the potential to generalize results of intensive smaller scale studies of mapped trees across broader extents, but also highlight the need to expand current networks to include forests in multiple stages of development. Further work is also needed to investigate spatial variation of forest dynamics across the region and elucidate drivers of mortality such as climatic anomalies and structural conditions (e.g. density). Finally, an individual tree-based approach examining size and species-specific mortality would strengthen inference on potential future resilience to drought and wildfire by providing information on compositional turnover and successional change.

Although there has been much concern regarding mortality associated with recent wildfire and drought, my analysis of this time period suggests these disturbance effects have been small at the scale of the entire Pacific Northwest. Wildfires and other agents of natural disturbance have increased structural diversity at the regional scale by creating diverse early successional habitat. There may be some ecological basis for the creation of diverse early successional habitat through management in portions of the region where wildfires have not occurred recently, but current trends suggest that wildfires have and will continue creating these habitats in the absence of proposed management activities (Franklin and Johnson 2012). Likewise, partial stand replacing fire and thinning from insects have begun restoring some aspects of historical structure by decreasing density and increasing the dominance of big trees, providing evidence of resilience of dry forests to these types of disturbances. It is evident that wildfires have already begun restoration, but the extent of restoration in wildfires is far less than the extent of densifying forest in later developmental stages. Relatively high proportions of stand-replacing fire in later developmental stages of dry vegetation zones indicate that these forests are currently at risk, but cumulative effects have thus far been small relative to their total extent.

The results of this study represent a snapshot of regional scale forest dynamics in the Pacific Northwest during a time of increasing wildfire and warming climatic trends. Although further work is needed to address uncertainties regarding variation at smaller spatial scales, this dissertation represents a new direction for assessing regional scale dynamics with increased ecological resolution and can serve as a baseline with which to compare future change in the Pacific Northwest and other regions around the world.

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Appendices

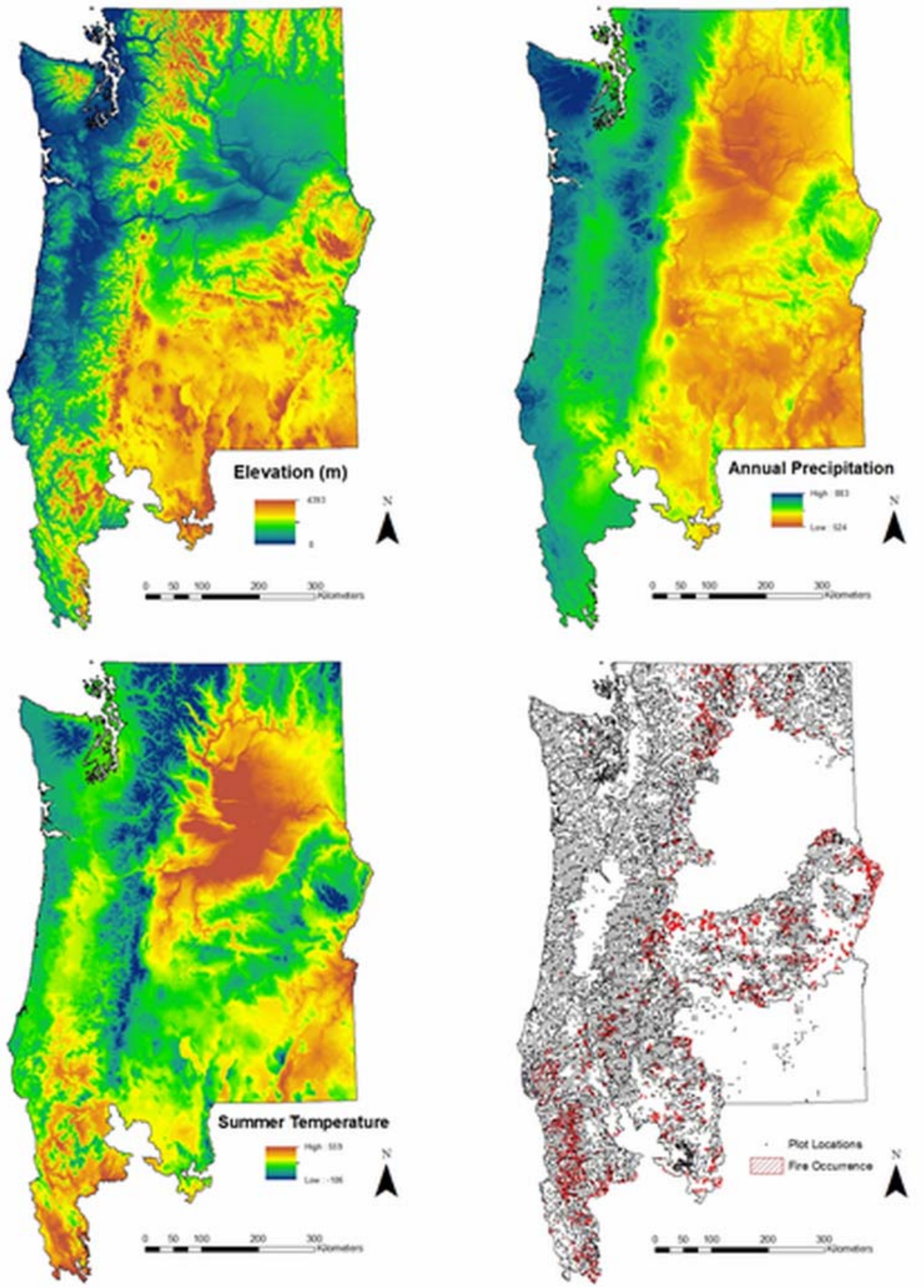


Fig. A-1.1 Map of study region in Oregon, Washington, and inland Northern California showing elevation, annual precipitation, temperature, and fuzzed locations of 11,091 FIA Annual plot locations with perimeters of wildfires ≥400 ha occurrence since 1984 overlaid.

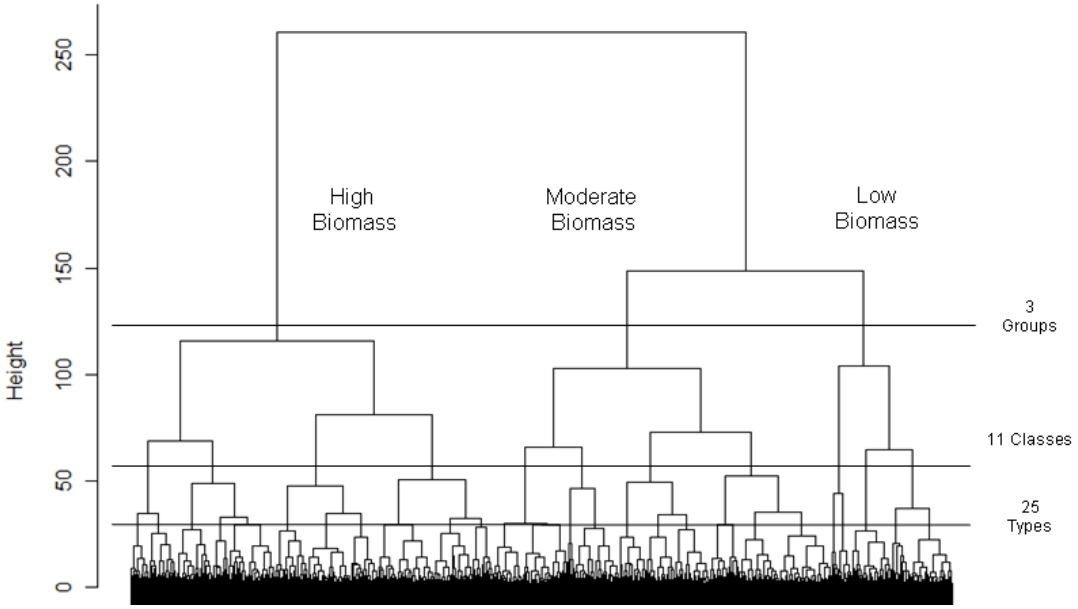


Figure A-1.2. Dendrogram with hierarchical classification of forest structural groups, classes, and types in the Pacific Northwest.

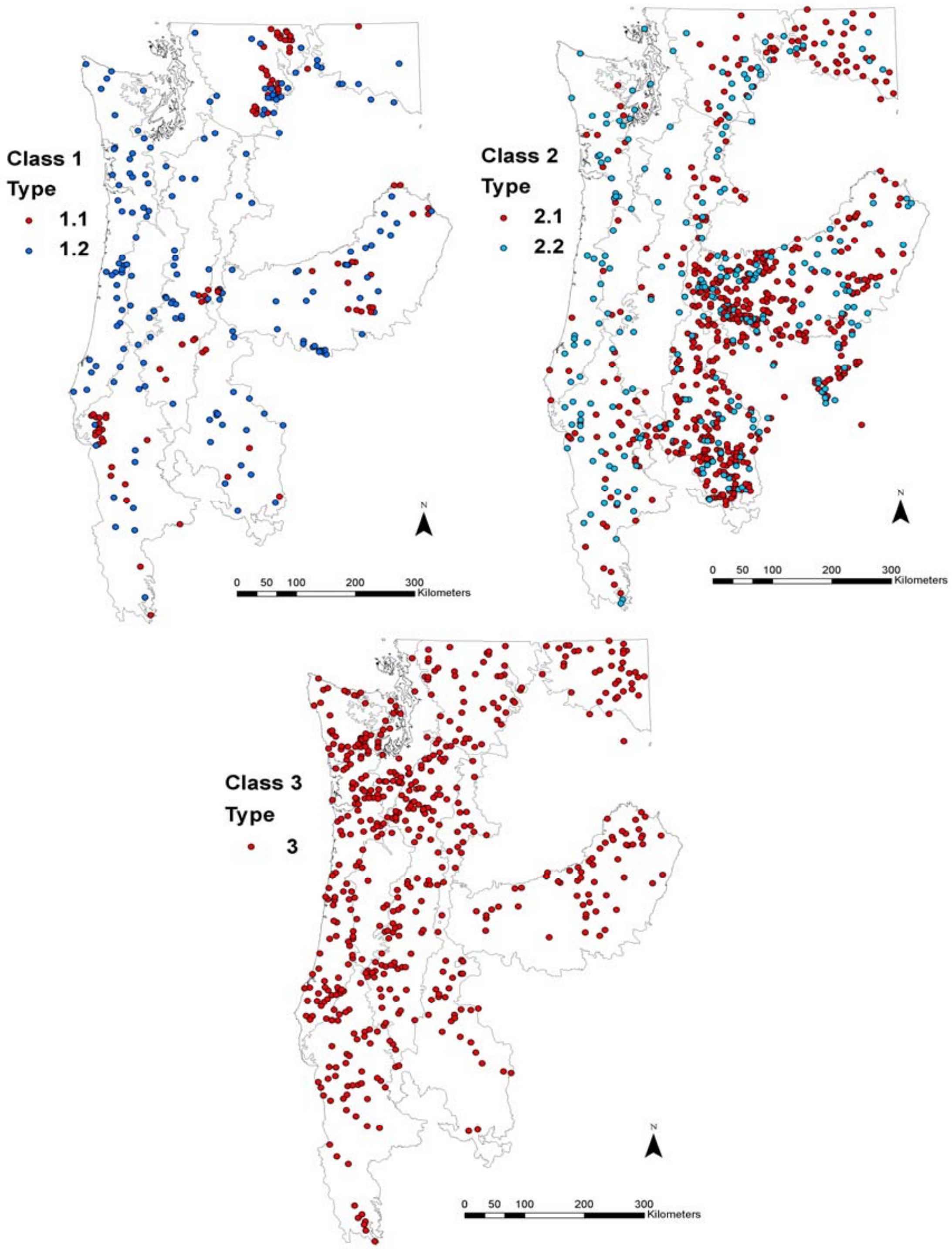


Fig. A-1.3 Geographic distributions of low biomass structural classes and types in the Pacific Northwest.

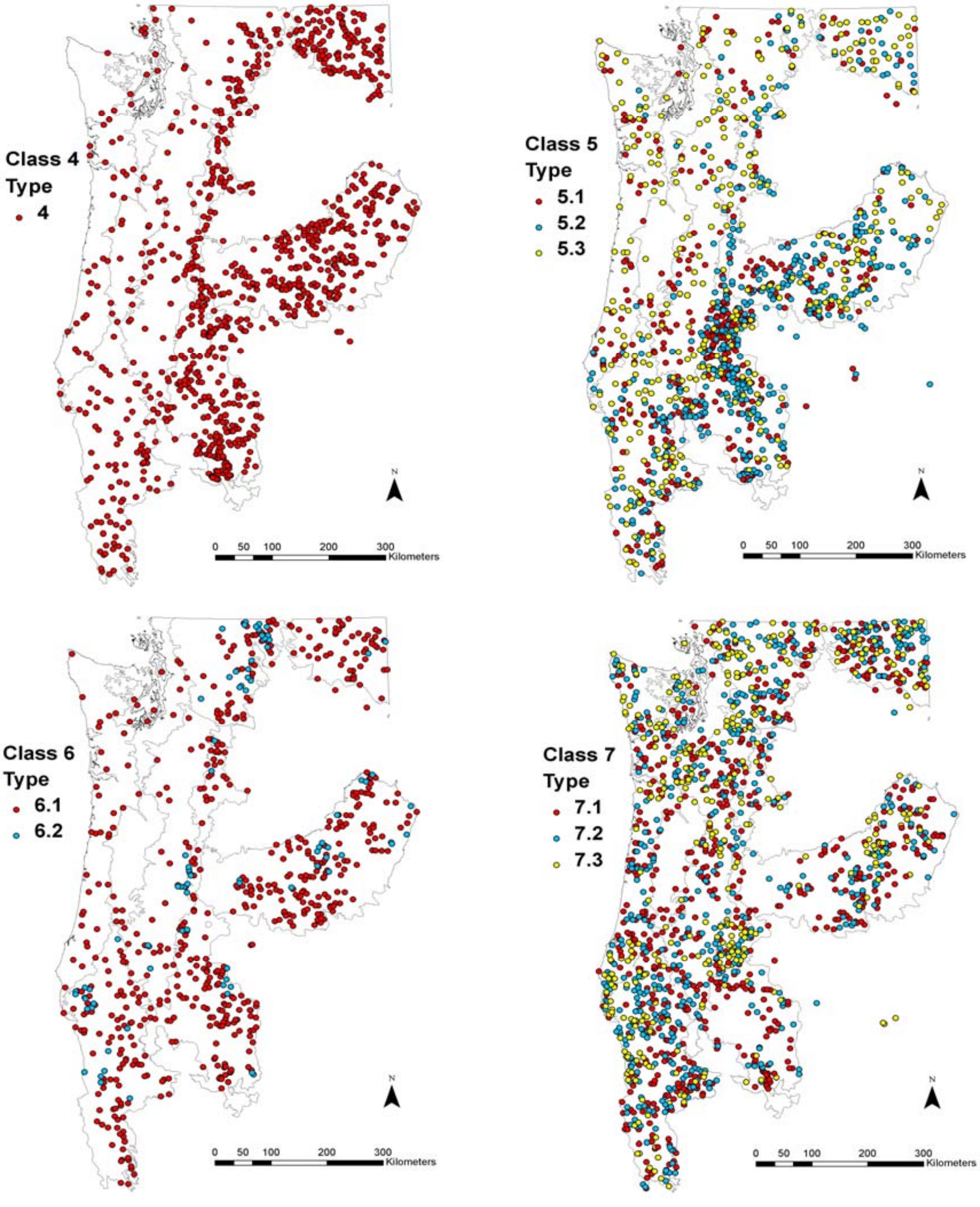


Fig. A-1.4. Geographic distributions of moderate biomass structural classes and types in the Pacific Northwest.

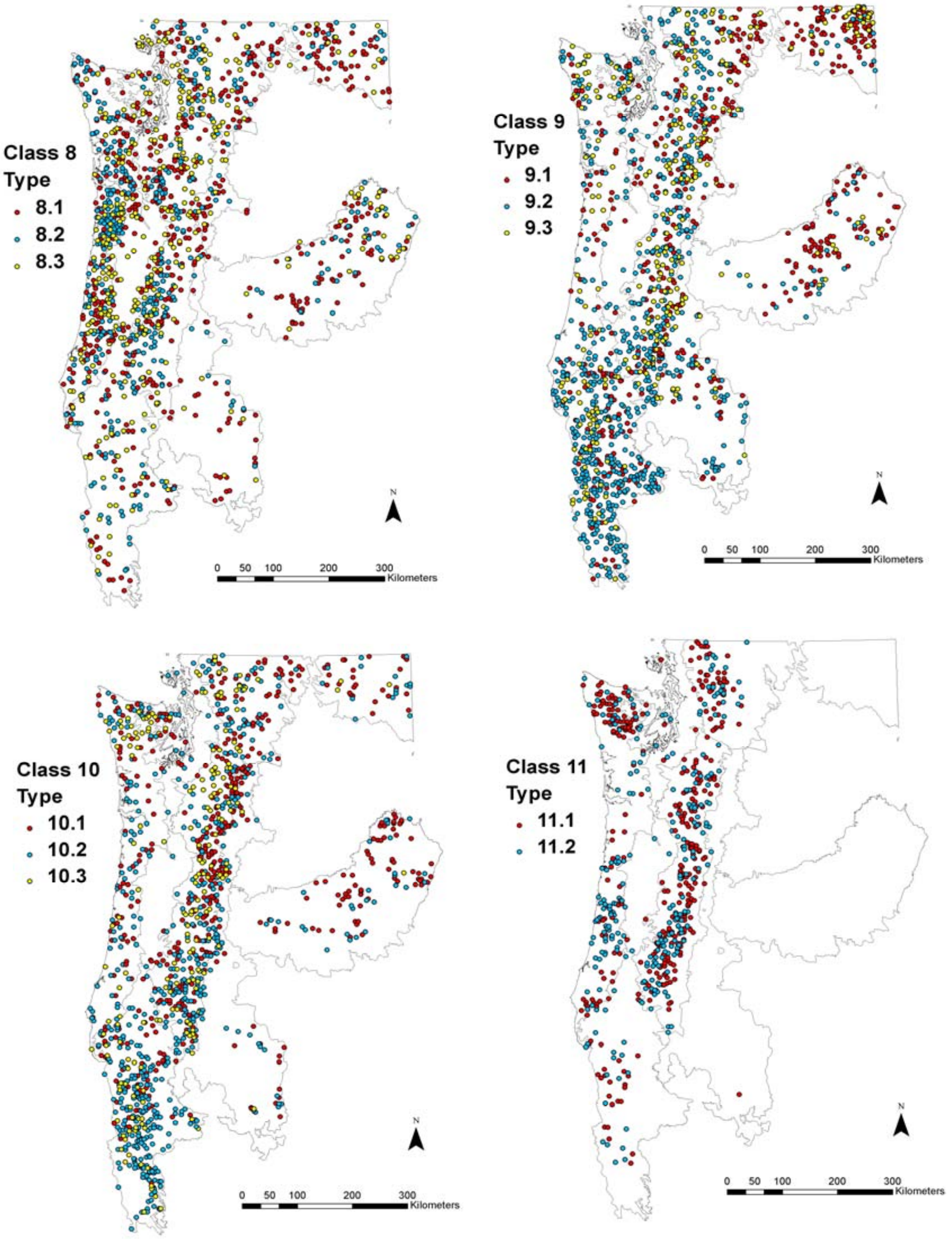
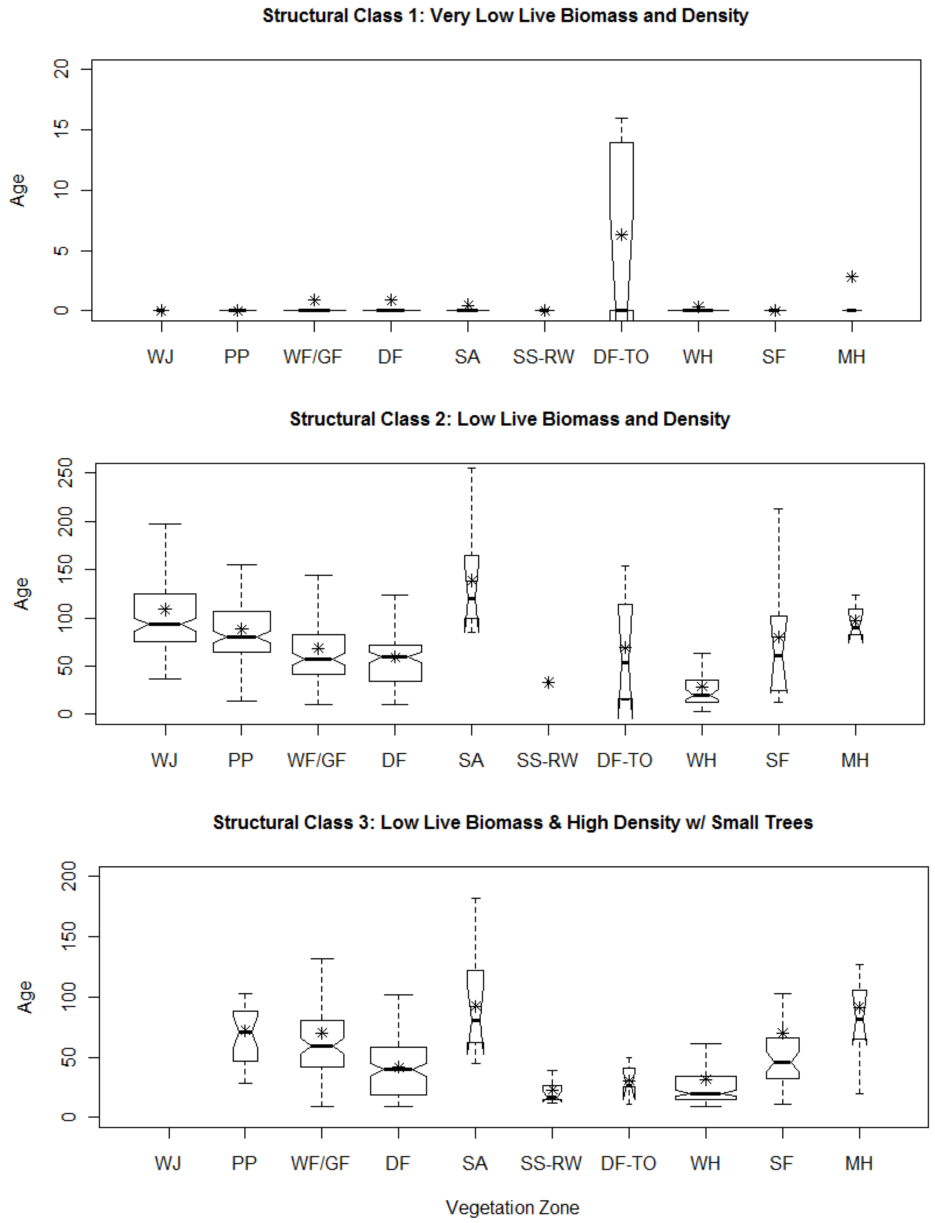


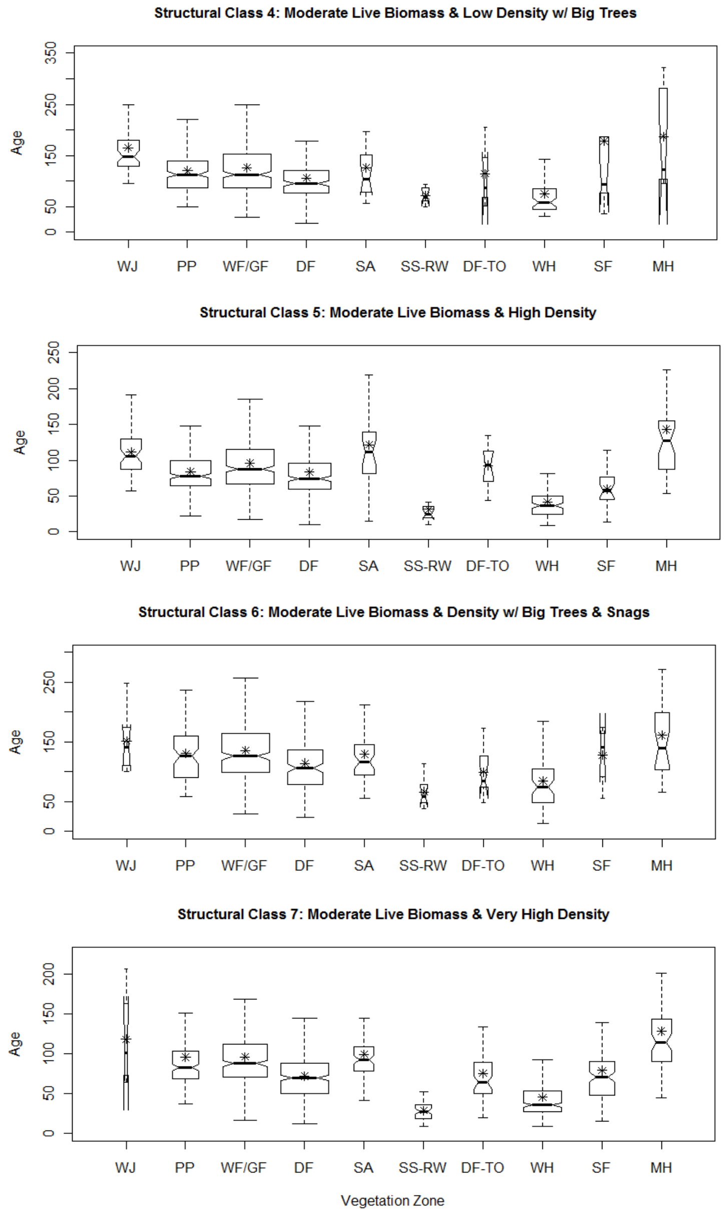
Fig. A-1.5. Geographic distributions of high biomass structural classes and types in the Pacific Northwest.


Structural Class 1: Very Low Live Biomass and Density

Structural Class 2: Low Live Biomass and Density

Structural Class 3: Low Live Biomass & High Density w/ Small Trees

Figure A-1.6. Mean age of dominant and co-dominant trees by vegetation zone for all very low biomass structural classes in the Pacific Northwest including (A) Class 1: Very Low Live Biomass and Density, (B) Class 2: Very Low Live Biomass and Density, (C) Class 3: Very Low Live Biomass and High Density. Vegetation zone names are abbreviated: WJ=Western Juniper, PP=Ponderosa Pine, WF/GF=White/Grand Fir, DF=Douglas-fir, SS-RW= Sitka Spruce – Redwood, DF-TO=Douglas-fir – Tanoak, WH=Western Hemlock, SF=Silver Fir, and MH=Mountain Hemlock. Width of each boxplot is proportional to the square root of the sample size and means are represented by an *.



Structural Class 4: Moderate Live Biomass & Low Density w/ Big Trees

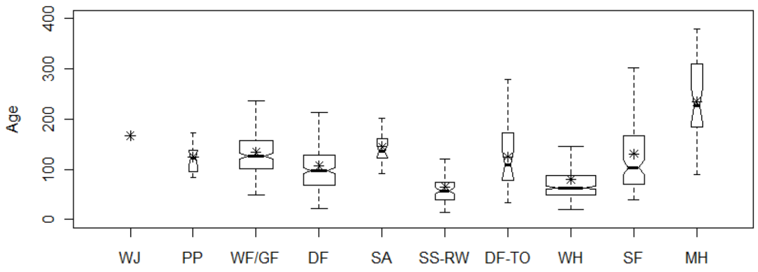
Structural Class 5: Moderate Live Biomass & High Density

Structural Class 6: Moderate Live Biomass & Density w/ Big Trees & Snags

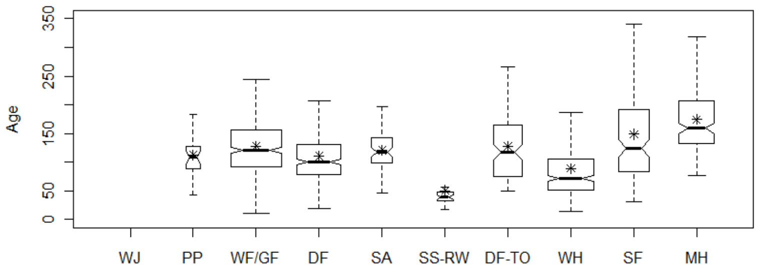
Structural Class 7: Moderate Live Biomass & Very High Density

Figure A-1.7. Mean age of dominant and co-dominant trees by vegetation zone for all low and moderate biomass structural classes in the Pacific Northwest including (A) Class 4: Low Live Biomass and Density w/ Big Trees, (B) Class 5: Low Live Biomass and Very High Density w/ Medium Trees, (C) Class 6: Moderate Live Biomass and Density w/ Big Trees, and (D) Moderate Live Biomass and Very High Density. Vegetation zone names are abbreviated: WJ=Western Juniper, PP=Ponderosa Pine, WF/GF=White/Grand Fir, DF=Douglas-fir, SS-RW= Sitka Spruce – Redwood, DF-TO=Douglas-fir – Tanoak, WH=Western Hemlock, SF=Silver Fir, and MH=Mountain Hemlock. Width of each boxplot is proportional to the square root of the sample size and means are represented by an *.

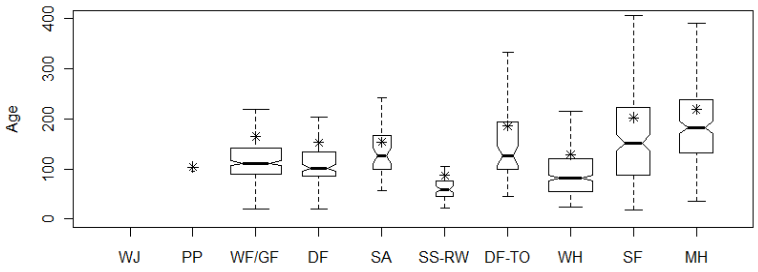
Structural Class 8: High Live Biomass & Density w/ Big Trees



Structural Class 9: High Live Biomass & Very High Density w/ Big Trees



Structural Class 10: Very High Live Biomass & High Density w/ Very Big Trees



Structural Class 11: Extremely High Live Biomass w/ Giant Trees

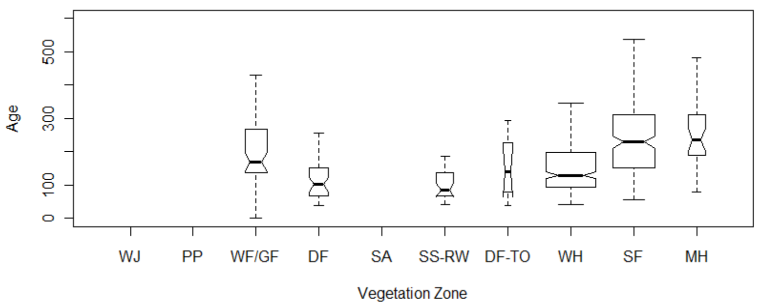


Figure A-1.8. Mean age of dominant and co-dominant trees by vegetation zone for all high biomass structural classes in the Pacific Northwest including (A) Class 8: High Live Biomass and Density w/ Big Trees, (B) Class 9: High Live Biomass and Very High Density w/Big Trees, (C) Class 10: Very High Live Biomass w/ Large Trees, and (D) Class 11: Extremely High Live Biomass w/ Giant Trees. Width of each boxplot is proportional to the square root of the sample size and means are represented by an *.

Table A-1.1. Mean and standard deviation of the twelve stand level attributes used in the hierarchical cluster analysis for eleven forest structural classes and twenty-five structural types in the Pacific Northwest.

Class/Type	Live Tree Biomass (Mg/ha)		Basal Area (m^2/ha)		Diameter Diversity Index		Stand Height (m)		Standard Deviation of DBH (cm)		Canopy Cover (%)		Quadratic Mean Diameter (cm)		Density (tph)		Snag Density (per ha)		Snag Biomass (Mg/ha)		Biomass of Dead/Downed Wood (Mg/ha)		Understory Cover (%)	
	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std
1	0.0	0.1	0.0	0.1	0.0	0.1	0.1	0.6	0.0	0.0	0.426	2.89	0.2	0.87	19	116	129	205	24	50	19	21	45	35
1.1	0.0	0.2	0.1	0.2	0.0	0.1	0.3	1.0	0.0	0.1	1	5	0.4	1.4	47	186	343	225	64	70	20	26	40	33
1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0	0	0.0	0.28	4	44	16	28.9	3	7	19	18	47	36
2	8	7	4	3	1.1	0.8	8	5	6	5	13	9	23	13	166	164	8	29.5	1	4	4	10	48	30
2.1	10	6	6	3	1.4	0.7	9	5	8	5	15	9	26	13	175	154	3	8.46	0.3	1	2	5	46	28
2.2	2	3	1	1	0.4	0.4	7	4	2	3	8	6	16	9	146	183	19	49.4	2	6	8	16	54	34
3 3.0	16	14	9	5	1.5	0.7	8	3	5	3	45	17	11	4	923	538	13	20.2	2	6	28	34	84	36
4 4.0	42	25	14	7	2.8	1.1	17	7	13	6	30	13	37	16	195	145	7	13	1	3	7	13	55	35
5	42	38	17	10	2.7	1.2	11	5	9	4	45	20	19	9	784	596	21	38.3	3	8	8	12	18	20
5.1	27	21	14	8	2.2	1.0	8	4	7	3	47	18	13	4	1,115	626	2	7.54	0.4	2	6	8	26	19
5.2	25	11	12	4	2.4	0.7	11	5	10	4	30	12	23	9	389	306	22	25.4	2	4	7	8	24	21
5.3	79	48	26	11	3.6	1.2	15	6	11	4	61	18	21	8	923	557	42	56.9	8	13	13	18	0	1
6	69	41	21	9	3.6	1.4	19	7	14	6	42	16	32	14	359	287	115	156	23	37	13	14	47	31
6.1	73	40	22	9	3.8	1.2	18	7	14	5	45	14	31	11	363	222	73	64.3	12	11	12	11	47	30
6.2	43	36	11	8	1.9	1.2	23	11	12	9	23	17	42	27	329	563	413	251	96	62	25	23	45	38
7	69	38	27	11	3.3	1.2	12	5	8	3	70	16	16	6	1,926	1,528	19	23.2	2	4	10	11	55	34
7.1	70	29	25	8	3.6	0.9	14	5	10	3	62	14	20	4	838	305	15	21.2	2	3	7	7	57	34
7.2	86	41	31	10	3.6	1.2	13	5	9	2	76	13	14	3	2,060	777	27	23.4	3	4	13	12	53	30
7.3	46	37	23	13	2.1	1.1	8	4	5	2	78	14	9	2	3,701	1,849	15	23.4	2	5	13	13	55	40
8	157	80	37	13	4.7	1.3	24	8	15	6	69	15	32	11	584	374	28	33.6	5	11	29	36	83	40
8.1	123	47	33	10	4.5	1.1	21	6	14	4	67	14	28	7	624	316	22	21	3	3	10	9	89	40
8.2	139	68	34	12	4.3	1.3	22	7	13	5	69	16	29	9	684	467	39	46	9	16	65	42	68	38
8.3	234	83	46	15	5.5	1.0	30	7	20	6	71	14	43	12	399	243	26	28	5	8	17	18	92	38
9	157	82	44	16	4.8	1.5	18	7	12	4	80	13	20	6	1,757	1,138	79	73.3	13	14	21	26	39	32
9.1	98	50	32	11	3.9	1.3	15	7	10	3	71	14	18	6	1,555	1,005	97	50	14	11	20	16	57	30
9.2	194	79	51	13	5.5	1.3	20	7	14	4	82	11	23	6	1,527	907	44	34.2	7	7	10	9	28	25
9.3	163	72	47	15	4.7	1.4	17	6	10	3	87	10	16	4	2,681	1,388	134	120	26	22	49	42	36	36
10	262	130	55	19	6.0	1.4	27	8	18	6	77	13	33	12	820	515	120	97.9	33	32	29	25	29	33
10.1	206	97	46	16	5.5	1.3	25	8	17	5	72	15	31	10	769	514	163	111	38	27	31	21	61	33
10.2	266	123	56	18	6.2	1.3	27	8	19	6	79	12	33	12	834	497	74	63.8	19	17	25	19	10	12
10.3	383	131	71	18	6.9	1.3	32	8	21	6	85	9	36	11	900	558	155	89.6	62	47	39	43	12	16
11	482	165	75	22	7.2	1.5	40	9	26	8	83	12	46	18	647	537	73	56.5	40	37	67	57	73	39
11.1	483	163	76	23	7.5	1.6	38	10	26	7	85	13	41	15	825	620	87	63.4	53	41	90	63	57	31
11.2	482	169	73	20	6.9	1.3	41	9	28	8	80	9	54	18	406	240	54	38.3	21	18	35	26	94	39

Table A-1.2. Relative abundance of eleven major structural classes and twenty-five structural types by vegetation zone (Simpson 2013) in the Pacific Northwest.

Class	Type	Wet					Dry					All
		Sitka Spruce/ Redwood	Douglas-fir/ Tanoak	Western Hemlock	Silver Fir	Mountain Hemlock	Western Juniper	Ponderosa Pine	Douglas-fir	White Fir /Grand Fir	Subalpine	
1		1.7%	2.2%	2.4%	0.8%	0.9%	1.1%	2.3%	2.2%	2.1%	7.0%	2.5%
	1.1	0.0%	1.9%	0.1%	0.1%	0.9%	0.0%	0.4%	1.1%	0.9%	5.8%	0.8%
	1.2	1.7%	0.3%	2.3%	0.6%	0.0%	1.1%	1.9%	1.1%	1.2%	1.2%	1.6%
2		0.3%	2.2%	1.9%	1.3%	1.3%	54.6%	15.3%	5.3%	4.3%	2.3%	7.4%
	2.1	0.3%	1.3%	0.4%	0.5%	1.1%	41.6%	12.2%	3.0%	2.9%	1.7%	5.0%
	2.2	0.0%	0.9%	1.5%	0.8%	0.2%	13.0%	3.2%	2.3%	1.5%	0.6%	2.3%
3	3.0	5.5%	1.6%	7.5%	5.7%	1.6%	0.0%	2.9%	6.7%	3.2%	3.2%	4.9%
4	4.0	1.7%	0.9%	2.6%	1.3%	1.3%	18.6%	21.6%	11.0%	9.9%	4.4%	8.9%
5		5.9%	4.1%	5.8%	3.3%	5.9%	21.2%	27.3%	12.0%	12.5%	7.6%	11.0%
	5.1	2.1%	0.3%	2.6%	1.4%	1.1%	8.9%	11.4%	2.8%	3.3%	2.3%	3.6%
	5.2	0.7%	0.6%	0.4%	0.5%	1.4%	11.9%	12.9%	4.5%	5.2%	2.3%	4.1%
	5.3	3.1%	3.1%	2.8%	1.4%	3.4%	0.4%	3.0%	4.6%	4.0%	2.9%	3.2%
6		2.4%	2.5%	2.7%	0.5%	4.5%	2.6%	8.7%	7.7%	11.3%	14.0%	6.3%
	6.1	2.4%	1.3%	2.5%	0.5%	3.2%	2.6%	8.6%	7.2%	9.7%	8.2%	5.5%
	6.2	0.0%	1.3%	0.1%	0.0%	1.3%	0.0%	0.1%	0.5%	1.6%	5.8%	0.8%
7		15.9%	19.7%	12.2%	14.4%	12.7%	1.5%	15.7%	20.4%	14.2%	20.7%	14.8%
	7.1	4.8%	3.8%	5.4%	5.1%	2.9%	0.7%	8.7%	9.8%	6.6%	6.4%	6.4%
	7.2	6.6%	7.8%	3.7%	4.6%	6.5%	0.0%	3.6%	6.4%	5.3%	7.3%	4.8%
	7.3	4.5%	8.1%	3.1%	4.7%	3.4%	0.7%	3.3%	4.2%	2.3%	7.0%	3.6%
8		26.9%	8.4%	25.9%	12.4%	5.4%	0.4%	2.3%	10.8%	10.2%	7.6%	12.5%
	8.1	10.0%	1.9%	8.3%	4.6%	2.5%	0.4%	1.9%	5.8%	5.1%	2.9%	5.2%
	8.2	9.7%	5.0%	10.1%	5.4%	1.4%	0.0%	0.4%	1.8%	3.1%	4.4%	4.0%
	8.3	7.2%	1.6%	7.6%	2.4%	1.4%	0.0%	0.0%	3.2%	2.0%	0.3%	3.3%
9		13.4%	35.6%	13.5%	16.7%	31.9%	0.0%	3.6%	14.0%	14.8%	19.2%	14.2%
	9.1	4.8%	4.1%	3.8%	4.2%	9.3%	0.0%	1.6%	4.2%	5.9%	13.4%	4.7%
	9.2	5.2%	25.6%	6.3%	7.4%	12.9%	0.0%	1.9%	8.9%	6.6%	1.5%	6.8%
	9.3	3.4%	5.9%	3.4%	5.1%	9.7%	0.0%	0.1%	1.0%	2.3%	4.4%	2.7%
10		15.5%	19.7%	13.4%	20.9%	29.0%	0.0%	0.1%	8.0%	15.2%	14.0%	12.1%
	10.1	4.1%	2.5%	5.7%	7.0%	10.8%	0.0%	0.0%	2.0%	6.0%	10.8%	4.4%
	10.2	8.3%	14.7%	5.6%	6.3%	11.8%	0.0%	0.1%	5.6%	7.6%	3.2%	5.7%
	10.3	3.1%	2.5%	2.1%	7.7%	6.5%	0.0%	0.0%	0.5%	1.7%	0.0%	1.9%
11		10.7%	3.1%	12.1%	22.7%	5.6%	0.0%	0.0%	1.9%	2.1%	0.0%	5.5%
	11.1	4.5%	1.6%	6.2%	17.1%	4.1%	0.0%	0.0%	0.7%	1.1%	0.0%	3.2%
	11.2	6.2%	1.6%	5.9%	5.6%	1.4%	0.0%	0.0%	1.2%	1.0%	0.0%	2.3%

Table A-1.3. Frequency of occurrence of eleven major structural classes and twenty-five structural types by vegetation zone (Simpson 2013) in the Pacific Northwest.

Class	Type	Wet Forests					Dry Forests				
		Sitka Spruce/ Redwood	Douglas-fir/ Tanoak	Western Hemlock	Silver Fir	Mountain Hemlock	Western Juniper	Ponderosa Pine	Douglas-fir	White Fir /Grand Fir	Subalpine
1		1.8%	2.6%	19.0%	2.2%	1.8%	1.1%	6.9%	16.1%	19.0%	8.8%
	1.1	0.0%	6.4%	2.1%	1.1%	5.3%	0.0%	3.2%	23.4%	24.5%	21.3%
	1.2	2.8%	0.6%	27.8%	2.8%	0.0%	1.7%	8.9%	12.2%	16.1%	2.2%
2		0.1%	0.9%	5.0%	1.2%	0.9%	18.0%	15.4%	12.9%	13.0%	1.0%
	2.1	0.2%	0.7%	1.6%	0.7%	1.1%	20.1%	17.9%	10.6%	12.5%	1.1%
	2.2	0.0%	1.2%	12.4%	2.3%	0.4%	13.6%	10.1%	17.8%	14.0%	0.8%
3	3.0	3.0%	0.9%	29.8%	8.3%	1.7%	0.0%	4.4%	24.4%	14.4%	2.0%
4	4.0	0.5%	0.3%	5.6%	1.0%	0.7%	5.1%	18.0%	22.2%	24.5%	1.5%
5		1.4%	1.1%	10.2%	2.1%	2.7%	4.7%	18.5%	19.5%	25.1%	2.1%
	5.1	1.5%	0.3%	13.8%	2.8%	1.5%	6.0%	23.6%	14.1%	20.4%	2.0%
	5.2	0.4%	0.4%	2.0%	0.9%	1.7%	7.0%	23.0%	19.6%	27.8%	1.7%
	5.3	2.5%	2.8%	16.7%	3.1%	5.3%	0.3%	6.9%	25.6%	26.9%	2.8%
6		1.0%	1.1%	8.1%	0.6%	3.6%	1.0%	10.3%	21.7%	39.3%	6.8%
	6.1	1.1%	0.7%	8.8%	0.7%	2.9%	1.1%	11.6%	23.3%	38.4%	4.6%
	6.2	0.0%	4.5%	3.4%	0.0%	8.0%	0.0%	1.1%	10.2%	45.5%	22.7%
7		2.8%	3.8%	15.9%	6.9%	4.3%	0.2%	7.9%	24.6%	21.1%	4.3%
	7.1	2.0%	1.7%	16.2%	5.6%	2.3%	0.3%	10.1%	27.3%	22.8%	3.1%
	7.2	3.5%	4.7%	14.7%	6.7%	6.7%	0.0%	5.6%	23.5%	24.0%	4.7%
	7.3	3.3%	6.6%	17.0%	9.4%	4.8%	0.5%	6.8%	21.3%	13.9%	6.1%
8		5.6%	1.9%	40.0%	7.0%	2.2%	0.1%	1.4%	15.5%	18.0%	1.9%
	8.1	5.0%	1.0%	30.8%	6.3%	2.4%	0.2%	2.8%	20.2%	21.7%	1.7%
	8.2	6.2%	3.6%	48.1%	9.4%	1.8%	0.0%	0.7%	7.8%	16.9%	3.3%
	8.3	5.8%	1.4%	44.5%	5.2%	2.2%	0.0%	0.0%	17.6%	13.5%	0.3%
9		2.5%	7.3%	18.4%	8.3%	11.3%	0.0%	1.9%	17.7%	23.0%	4.2%
	9.1	2.7%	2.5%	15.7%	6.4%	10.1%	0.0%	2.5%	16.1%	27.7%	8.9%
	9.2	2.0%	10.9%	17.9%	7.7%	9.5%	0.0%	2.1%	23.3%	21.5%	0.7%
	9.3	3.3%	6.3%	24.3%	13.3%	18.0%	0.0%	0.3%	6.3%	19.0%	5.0%
10		3.4%	4.7%	21.4%	12.2%	12.1%	0.0%	0.1%	11.9%	27.8%	3.6%
	10.1	2.4%	1.6%	24.8%	11.2%	12.2%	0.0%	0.0%	7.9%	29.7%	7.5%
	10.2	3.8%	7.4%	18.8%	7.7%	10.4%	0.0%	0.2%	17.5%	29.2%	1.7%
	10.3	4.2%	3.8%	21.1%	28.2%	16.9%	0.0%	0.0%	4.2%	19.2%	0.0%
11		5.1%	1.6%	42.3%	29.1%	5.1%	0.0%	0.0%	6.2%	8.5%	0.0%
	11.1	3.7%	1.4%	37.8%	38.1%	6.5%	0.0%	0.0%	4.0%	7.7%	0.0%
	11.2	6.9%	1.9%	48.5%	16.9%	3.1%	0.0%	0.0%	9.2%	9.6%	0.0%

Table A-1.4. Live tree size class distributions by forest structural class and type in the Pacific Northwest.

		Live Trees/ha													
Class	Type	<10		10 to 25		25 to 50		50 to 75		75 to 100		100 to 150		>150	
		Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev
1		19.0	116.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	1.1	47.3	186.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	1.2	4.2	44.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2		70.6	146.1	71.3	86.6	22.7	27.1	1.2	3.3	0.2	0.9	0.0	0.2	0.0	0.0
	2.1	55.1	117.3	87.5	93.5	30.7	28.8	1.6	3.8	0.4	1.1	0.0	0.3	0.0	0.0
	2.2	104.2	190.4	36.2	55.1	5.6	10.0	0.2	1.5	0.0	0.3	0.0	0.0	0.0	0.0
3		636.6	539.6	265.2	241.0	20.3	32.0	0.6	2.8	0.3	1.1	0.0	0.3	0.0	0.2
	3	636.6	539.6	265.2	241.0	20.3	32.0	0.6	2.8	0.3	1.1	0.0	0.3	0.0	0.2
4		35.2	92.2	72.8	78.8	70.5	57.6	13.6	16.2	2.5	5.1	0.3	1.3	0.0	0.3
	4	35.2	92.2	72.8	78.8	70.5	57.6	13.6	16.2	2.5	5.1	0.3	1.3	0.0	0.3
5		418.5	514.6	278.2	257.2	79.6	73.9	6.5	13.6	1.0	2.6	0.1	0.8	0.0	0.2
	5.1	722.5	611.1	344.4	287.3	44.8	48.3	2.8	6.9	0.6	1.6	0.1	0.5	0.0	0.2
	5.2	152.9	247.7	164.8	147.1	66.0	45.6	4.3	7.0	0.7	2.0	0.1	0.5	0.0	0.0
	5.3	421.8	461.9	349.8	280.8	135.5	92.5	13.4	21.1	1.8	3.6	0.3	1.2	0.0	0.3
6		97.7	227.1	142.6	141.2	97.2	69.8	17.0	19.1	3.3	5.2	0.8	2.2	0.0	0.3
	6.1	85.7	166.3	149.2	126.9	105.4	67.6	18.3	19.7	3.5	5.3	0.8	2.3	0.0	0.2
	6.2	181.2	461.0	96.6	211.6	40.1	57.1	8.0	11.7	2.2	4.1	0.7	1.8	0.1	0.6
7		1299.5	1447.3	501.8	408.7	115.0	90.7	8.2	13.4	1.4	3.4	0.3	1.3	0.0	0.3
	7.1	337.3	312.9	344.5	202.3	144.7	90.4	9.6	13.3	1.3	2.8	0.3	1.0	0.0	0.2
	7.2	1297.2	765.7	623.0	385.6	126.3	84.2	10.4	15.4	2.1	4.5	0.5	1.7	0.0	0.3
	7.3	3031.9	1753.0	619.9	584.1	46.1	58.1	2.4	8.1	0.6	2.1	0.2	1.3	0.0	0.2
8		175.2	284.4	195.1	181.7	172.9	108.2	34.1	35.5	5.7	8.9	1.6	3.8	0.1	0.7
	8.1	190.7	260.1	219.6	174.6	183.9	103.7	25.7	23.6	3.2	5.4	0.7	1.9	0.1	0.5
	8.2	233.9	364.7	233.8	211.5	190.0	115.2	22.6	25.0	3.5	6.4	1.2	3.1	0.1	0.6
	8.3	78.3	154.7	108.6	111.7	134.3	96.5	61.8	46.0	12.3	12.0	3.7	5.6	0.2	1.0
9		1017.2	1024.2	516.8	377.9	189.4	121.1	26.1	28.5	5.2	7.6	2.1	4.4	0.1	0.6
	9.1	928.2	1021.9	456.5	326.4	154.2	101.9	13.6	17.1	2.1	4.0	0.5	1.8	0.0	0.2
	9.2	792.0	793.6	475.7	334.9	211.7	122.1	36.9	32.1	7.7	8.7	3.0	5.2	0.2	0.8
	9.3	1736.4	1208.0	724.0	479.6	193.8	134.6	20.4	23.8	4.2	7.0	2.4	4.5	0.2	0.8
10		301.3	414.6	257.9	214.7	189.9	123.3	52.3	40.9	13.1	14.9	5.4	8.2	0.4	1.5
	10.1	280.8	419.2	241.2	203.6	190.3	121.5	44.3	33.9	9.2	10.4	2.7	4.6	0.2	0.9
	10.2	296.9	368.9	277.6	227.2	187.8	124.3	50.6	38.9	14.3	17.1	6.0	8.4	0.5	1.8
	10.3	361.8	516.8	237.8	196.4	195.3	124.4	75.7	51.7	18.3	14.4	9.8	11.3	0.8	1.9
11		257.1	417.2	163.9	182.0	113.4	87.9	70.0	57.2	24.9	17.7	15.6	13.2	2.2	4.1
	11.1	377.0	496.7	212.1	212.1	128.2	99.6	66.7	55.9	23.1	17.7	15.7	12.1	2.5	4.1
	11.2	94.7	173.6	98.7	98.8	93.4	63.8	74.5	58.7	27.3	17.4	15.4	14.6	1.7	4.2

Table A-1.5. Snag size class distributions by forest structural class and type in the Pacific Northwest.

Class	Type	Snags/ha									
		12 to 25		25 to 50		50 to 75		75 to 100		>100	
		Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev
1		78.4	153.0	43.1	68.8	5.6	13.7	0.9	2.9	0.6	2.8
	1.1	215.0	198.4	110.9	79.5	14.0	20.1	2.1	4.5	1.3	4.6
	1.2	7.1	19.2	7.6	15.7	1.2	4.5	0.2	0.8	0.2	0.8
2		5.2	24.1	2.2	10.9	0.4	3.0	0.1	0.9	0.0	0.5
	2.1	2.1	7.3	0.7	3.6	0.1	1.1	0.0	0.3	0.0	0.4
	2.2	11.9	40.8	5.2	18.2	1.1	5.0	0.3	1.5	0.1	0.7
3		7.3	14.5	4.0	9.6	0.9	3.7	0.4	1.7	0.3	1.3
	3	7.3	14.5	4.0	9.6	0.9	3.7	0.4	1.7	0.3	1.3
4		4.1	10.2	2.1	6.3	0.6	2.6	0.2	0.7	0.0	0.4
	4	4.1	10.2	2.1	6.3	0.6	2.6	0.2	0.7	0.0	0.4
5		14.7	31.4	5.2	12.2	1.0	4.1	0.2	0.9	0.1	0.9
	5.1	1.3	6.7	0.4	2.6	0.1	0.8	0.1	0.5	0.0	0.3
	5.2	15.5	22.2	5.4	10.0	1.0	3.5	0.2	0.9	0.1	0.5
	5.3	28.5	47.6	10.3	17.9	2.1	6.1	0.4	1.2	0.3	1.5
6		71.2	116.9	35.6	58.6	6.7	15.4	1.4	3.8	0.6	2.2
	6.1	45.4	56.6	21.7	25.7	4.1	8.3	1.0	2.5	0.4	1.5
	6.2	251.2	223.6	132.1	110.5	24.2	32.7	4.2	7.8	1.8	4.6
7		13.7	20.7	4.3	9.1	0.9	3.4	0.3	1.0	0.1	0.6
	7.1	11.1	18.7	3.6	8.2	0.6	2.5	0.2	0.8	0.1	0.5
	7.2	19.2	22.2	6.2	10.3	1.3	4.1	0.4	1.2	0.2	0.8
	7.3	11.0	20.5	3.2	8.3	0.9	3.8	0.2	0.9	0.1	0.7
8		17.1	25.0	7.9	16.0	2.0	6.3	0.8	2.3	0.6	1.7
	8.1	15.1	19.4	4.8	8.9	1.2	4.1	0.3	1.1	0.2	0.9
	8.2	21.7	32.1	12.4	23.1	3.0	8.1	1.3	3.1	0.9	2.1
	8.3	14.7	22.0	7.4	12.6	2.0	6.3	0.9	2.3	0.7	2.0
9		52.7	63.3	20.4	30.0	4.1	8.5	1.1	2.5	0.6	1.7
	9.1	65.5	52.0	26.5	26.4	4.2	8.3	0.8	2.0	0.4	1.4
	9.2	29.8	30.7	10.2	15.3	2.9	6.6	0.9	1.9	0.4	1.3
	9.3	88.0	105.5	35.5	48.6	7.0	11.6	2.0	3.8	1.3	2.5
10		69.5	80.9	36.1	39.2	9.7	16.5	3.0	4.9	1.6	3.2
	10.1	94.2	97.3	51.8	46.9	12.5	20.9	3.0	5.1	1.5	2.9
	10.2	44.9	54.4	20.4	24.3	6.0	10.3	2.2	3.7	1.0	2.2
	10.3	85.6	84.1	46.8	37.5	14.0	17.5	5.4	6.5	3.7	5.1
11		29.4	41.7	23.2	25.4	11.0	15.6	5.3	6.2	4.4	5.5
	11.1	34.2	48.6	25.9	27.8	14.4	17.9	7.1	6.9	5.6	6.0
	11.2	22.8	28.8	19.7	21.4	6.4	10.1	2.8	3.7	2.7	4.1

Table A-1.6. Size class distribution of biomass of dead and downed wood by forest structural class and type in the Pacific Northwest.

Biomass of Dead and Downed Wood (Mg/ha)											
Class	Type	12 to 25 cm		25 to 50 cm		50 to 75 cm		75 to 100 cm		>100 cm	
		Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev
1		5.0	6.0	8.5	10.8	3.0	6.3	1.8	6.2	0.9	8.0
	1.1	5.3	6.7	10.1	12.6	2.4	5.6	1.4	7.0	1.2	11.9
	1.2	4.8	5.5	7.6	9.6	3.3	6.6	2.0	5.7	0.8	4.9
2		1.1	2.9	1.5	3.7	0.9	3.8	0.5	3.8	0.1	1.6
	2.1	0.1	1.6	0.8	2.1	0.6	2.6	0.2	1.8	0.1	1.2
	2.2	2.3	4.3	3.1	5.6	1.6	5.5	1.2	6.3	0.3	2.3
3		3.7	4.4	6.4	8.0	6.9	12.8	5.5	11.9	5.4	18.8
	3	3.7	4.4	6.4	8.0	6.9	12.8	5.5	11.9	5.4	18.8
4		1.6	3.6	2.3	4.0	1.6	4.5	1.2	5.8	0.6	4.7
	4	1.6	3.6	2.3	4.0	1.6	4.5	1.2	5.8	0.6	4.7
5		2.1	4.1	3.1	5.2	1.8	4.4	1.0	4.7	0.3	2.7
	5.1	1.8	3.1	2.3	3.5	1.1	3.2	0.8	3.8	0.1	0.7
	5.2	1.6	2.4	2.8	4.4	1.4	3.4	0.6	2.9	0.1	1.7
	5.3	3.1	6.1	4.5	7.1	2.9	6.1	1.8	6.9	0.6	4.4
6		3.1	4.2	5.7	6.4	2.5	5.2	1.4	4.8	0.6	3.5
	6.1	2.7	3.2	4.8	5.3	2.3	4.4	1.2	4.3	0.6	3.3
	6.2	6.3	7.8	11.5	9.5	3.8	8.6	2.6	7.3	0.8	4.6
7		2.3	3.1	3.9	5.2	2.3	4.6	1.2	4.3	0.5	3.3
	7.1	1.6	2.1	2.5	3.2	1.6	3.5	0.7	3.2	0.3	2.6
	7.2	2.6	3.4	4.9	5.9	3.0	5.3	1.6	5.0	0.7	3.8
	7.3	3.2	3.8	4.9	6.5	2.6	5.1	1.6	5.0	0.6	3.6
8		2.9	3.7	7.1	8.8	7.3	11.8	6.3	17.8	5.6	17.4
	8.1	2.1	2.3	3.8	4.5	2.3	4.2	1.2	4.2	0.4	3.3
	8.2	4.7	5.1	12.9	11.4	15.9	15.6	15.6	27.9	15.7	27.4
	8.3	2.2	2.5	5.2	6.5	4.8	8.1	3.1	7.6	1.5	6.0
9		3.6	4.8	7.0	8.3	4.6	9.1	2.8	8.3	2.6	11.7
	9.1	5.5	6.5	8.5	8.2	3.3	5.5	1.9	5.8	0.9	4.7
	9.2	1.8	2.0	3.9	4.3	2.6	4.6	1.1	3.5	0.5	3.3
	9.3	4.7	4.7	12.5	11.9	11.7	16.3	9.0	145.9	11.0	23.7
10		4.0	4.4	10.4	10.2	7.2	10.4	4.5	9.6	3.1	12.0
	10.1	5.1	5.3	12.7	11.8	7.1	9.6	3.5	8.4	2.4	9.0
	10.2	3.3	3.7	8.5	7.9	6.2	8.5	4.6	9.0	2.3	8.0
	10.3	3.7	3.2	11.1	11.2	10.8	15.4	6.7	12.9	7.0	22.6
11		2.8	3.0	13.4	10.5	17.2	16.8	15.1	19.3	18.2	37.4
	11.1	3.3	3.3	16.4	11.2	23.2	18.2	20.2	21.0	27.0	45.8
	11.2	2.2	2.4	9.5	7.9	9.0	9.9	8.1	14.2	6.4	15.0

Table A-1.7. Breakdown of the percentage of total understory cover by shrubs, forbs, and graminoids by forest structural class and type in the Pacific Northwest.

% Understory Cover									
Class	Type	Forbs		Shrubs		Graminoids		All Understory	
		Mean	Stdev	Mean	Stdev	Mean	Stdev	Mean	Stdev
1		14.1	16.9	18.6	21.3	12.0	16.3	44.7	35.4
	1.1	11.0	11.8	19.3	21.9	10.1	14.0	40.4	33.4
	1.2	15.7	18.8	18.3	21.0	13.0	17.3	46.9	36.3
2		10.1	11.9	18.7	20.7	19.4	17.7	48.2	30.0
	2.1	8.9	9.9	16.1	17.9	20.5	17.9	45.6	27.5
	2.2	12.6	15.1	24.4	24.9	17.0	16.9	53.9	34.2
3		22.2	18.7	47.4	30.1	14.0	17.7	83.6	35.8
	3	22.2	18.7	47.4	30.1	14.0	17.7	83.6	35.8
4		12.3	13.6	21.2	22.2	21.6	20.4	55.1	35.1
	4	12.3	13.6	21.2	22.2	21.6	20.4	55.1	35.1
5		3.8	6.0	7.8	11.5	6.2	10.2	17.9	20.2
	5.1	5.3	5.9	13.0	13.0	8.1	10.4	26.3	18.8
	5.2	5.5	7.0	9.4	11.5	9.5	11.9	24.4	20.7
	5.3	0.1	0.4	0.1	0.6	0.1	0.4	0.3	1.2
6		13.4	13.7	20.9	21.4	12.4	14.0	46.8	30.7
	6.1	13.0	12.5	21.3	21.5	12.9	13.9	47.1	29.5
	6.2	16.9	19.8	18.6	20.5	9.1	14.1	44.7	38.0
7		14.1	15.1	31.5	26.6	9.5	14.0	55.1	34.5
	7.1	14.0	14.8	31.4	27.2	11.6	14.9	57.0	34.4
	7.2	14.2	14.6	30.9	24.5	7.8	12.4	52.9	30.3
	7.3	14.3	16.1	32.4	28.2	8.1	13.8	54.8	39.5
8		29.5	25.1	45.1	30.9	8.5	14.9	83.0	40.1
	8.1	29.1	26.0	47.6	32.4	12.3	17.9	89.0	39.9
	8.2	26.5	21.2	36.9	26.4	5.0	10.8	68.3	38.0
	8.3	33.8	27.5	51.1	31.4	6.7	12.4	91.6	37.9
9		11.9	15.1	22.8	22.4	4.3	8.1	39.1	31.8
	9.1	16.6	16.2	32.5	23.9	8.0	11.4	57.2	29.7
	9.2	8.5	10.9	16.8	19.1	2.5	4.7	27.8	25.0
	9.3	12.6	19.4	21.3	21.8	2.3	5.3	36.2	36.1
10		11.0	16.2	16.2	22.9	2.2	5.2	29.4	33.3
	10.1	22.7	20.5	34.2	28.1	4.5	7.6	61.5	33.1
	10.2	3.9	6.0	5.4	7.4	1.0	2.1	10.3	11.9
	10.3	4.8	8.0	6.7	11.0	0.4	1.5	12.0	16.0
11		30.4	26.1	41.1	29.0	1.3	3.3	72.8	39.1
	11.1	24.2	18.6	32.1	24.4	0.9	2.2	57.2	31.0
	11.2	38.7	31.9	53.3	30.3	1.9	4.3	93.9	39.1

Table A-2.1. Confusion matrix with predicted class accuracies for 11 major structural classes (This dissertation, Chapter 2).

Structural Class	1	2	3	4	5	6	7	8	9	10	11	Class Error
1	269	5	0	0	0	0	0	0	0	0	0	1.8%
2	0	735	21	32	22	4	2	0	0	0	0	9.9%
3	0	25	428	11	28	3	40	6	0	0	0	20.9%
4	0	32	5	861	26	22	25	15	0	2	0	12.9%
5	0	24	26	53	975	19	90	0	22	9	0	20.0%
6	0	8	4	24	24	520	10	53	28	31	0	25.9%
7	0	0	26	29	39	4	1389	45	110	0	0	15.4%
8	0	0	3	28	5	40	77	1119	59	39	18	19.4%
9	0	0	11	0	7	17	88	62	1292	90	4	17.8%
10	0	0	0	2	6	31	0	22	113	1117	48	16.6%
11	0	0	0	0	0	2	0	19	6	68	517	15.5%

Table A-2.2. Results of pairwise tests for differences in the cumulative distribution functions of mortality rates among disturbances in the Pacific Northwest (ns=not significant,*<0.05, **<0.01, ***<0.001, ****<0.0001).

	None	Pathogen	Insect/ Pathogen	Insect	Fire/ Insect	Fire	Wind
None	-	****	****	****	****	****	****
Pathogen	-	-	****	***	****	****	****
Insect/ Pathogen	-	-	-	ns	****	****	****
Insect	-	-	-	-	****	****	****
Fire/ Insect	-	-	-	-	-	ns	****
Fire	-	-	-	-	-	-	****
Wind	-	-	-	-	-	-	-

Table A-2.3. Results of pairwise tests for differences in the cumulative distribution functions of mortality rates among vegetation zones in the Pacific Northwest (ns=not significant, *<0.05, **<0.01, ***<0.001, ****<0.0001).

	WH	SF	MH	SA	GF/WF	DF	PP
WH	-	ns	*	*	**	****	****
SF	-	-	ns	***	**	****	****
MH	-	-	-	***	**	***	****
SA	-	-	-	-	ns	**	****
GF/WF	-	-	-	-	-	**	****
DF	-	-	-	-	-	-	****
PP	-	-	-	-	-	-	-

Table A-2.4. Results of pairwise tests for differences in the cumulative distribution functions of mortality rates among developmental stages in the western hemlock vegetation zone (ns=not significant, *<0.05, **<0.01, ***<0.001, ****<0.0001).

	Early	Mid	Mature	Late	Old Growth
Early	-	ns	**	***	*
Mid	-	-	ns	*	ns
Mature	-	-	-	*	**
Late	-	-	-	-	ns
Old Growth	-	-	-	-	-

Table A-2.5. Results of pairwise tests for differences in the cumulative distribution functions of mortality rates among developmental stages in the silver fir vegetation zone (ns=not significant, *<0.05, **<0.01, ***<0.001, ****<0.0001).

	Early	Mid	Mature	Late	Old-Growth
Early	-	ns	ns	***	ns
Mid	-	-	ns	****	ns
Mature	-	-	-	ns	ns
Late	-	-	-	-	*
Old-Growth	-	-	-	-	-

Table A-2.6. Results of pairwise tests for differences in the cumulative distribution functions of mortality rates among developmental stages in the mountain hemlock vegetation zone (ns=not significant,*<0.05, **<0.01, ***<0.001, ****<0.0001).

	Early	Mid	Mature	Late	Old-Growth
Early	-	ns	ns	ns	*
Mid	-	-	ns	ns	ns
Mature	-	-	-	ns	ns
Late	-	-	-	-	ns
Old-Growth	-	-	-	-	-

Table A-2.7. Results of pairwise tests for differences in the cumulative distribution functions of mortality rates among developmental stages in the subalpine vegetation zone (ns=not significant, *<0.05, **<0.01, ***<0.001, ****<0.0001).

	Early	Mid	Mature	Late	Old-Growth
Early	-	ns	****	****	****
Mid	-	-	ns	**	**
Mature	-	-	-	*	ns
Late	-	-	-	-	ns
Old-Growth	-	-	-	-	-

Table A-2.8. Results of pairwise tests for differences in the cumulative distribution functions of mortality rates among developmental stages in the grand fir/white fir vegetation zone (ns=not significant, *<0.05, **<0.01, ***<0.001, ****<0.0001).

	Early	Mid	Mature	Late	Old-Growth
Early	-	ns	ns	***	****
Mid	-	-	ns	*	****
Mature	-	-	-	****	****
Late	-	-	-	-	ns
Old-Growth	-	-	-	-	-

Table A-2.9. Results of pairwise tests for differences in the cumulative distribution functions of mortality rates among developmental stages in the Douglas-fir vegetation zone (ns=not significant, *<0.05, **<0.01, ***<0.001, ****<0.0001).

	Early	Mid	Mature	Late	Old-Growth
Early	-	ns	ns	ns	ns
Mid	-	-	*	**	****
Mature	-	-	-	**	*
Late	-	-	-	-	ns
Old-Growth	-	-	-	-	-

Table A-2.10. Results of pairwise tests for differences in the cumulative distribution functions of mortality rates among developmental stages in the ponderosa pine vegetation zone (ns=not significant, *<0.05, **<0.01, ***<0.001, ****<0.0001).

	Early	Mid	Mature	Late	Old-Growth
Early	-	ns	ns	ns	ns
Mid	-	-	ns	****	****
Mature	-	-	-	****	****
Late	-	-	-	-	ns
Old-Growth	-	-	-	-	-

Table A-2.11. Proportion of the western hemlock vegetation zone in the Pacific Northwest by stage of structural development and mortality level classified into one of four trajectories of structural change based on changes density of trees per ha and quadratic mean diameter where: “densifying”: $\Delta TPH \geq 0$ and $\Delta QMD < 0$, “aggrading”: $\Delta TPH \geq 0$ and $\Delta QMD \geq 0$, “die-back”: $\Delta TPH < 0$ and $\Delta QMD < 0$, and “thinning”: $\Delta TPH < 0$ and $\Delta QMD > 0$.

Stage	Western Hemlock				
	Densifying	Aggrading	Thinning	Die-back	All
Early	0.0	2.0	0.9	0.0	2.9
<0.5	0.0	1.4	0.3	0.0	1.6
0.5-0.99	0.0	0.3	0.3	0.0	0.6
1-2.49	0.0	0.3	0.3	0.0	0.6
2.5-4.99	0.0	0.0	0.0	0.0	0.0
5-9.99	0.0	0.0	0.0	0.0	0.0
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
Mid	2.2	4.7	8.3	0.3	15.5
<0.5	0.8	2.0	0.9	0.0	3.6
0.5-0.99	1.0	1.6	0.9	0.0	3.4
1-2.49	0.3	0.9	2.8	0.0	3.9
2.5-4.99	0.3	0.3	2.3	0.3	3.1
5-9.99	0.0	0.0	1.4	0.0	1.4
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
Mature	4.1	6.0	26.2	1.0	37.4
<0.5	1.3	3.1	2.1	0.1	6.6
0.5-0.99	0.8	1.8	5.2	0.3	8.0
1-2.49	1.9	1.0	12.6	0.0	15.5
2.5-4.99	0.2	0.1	5.0	0.6	5.9
5-9.99	0.0	0.0	1.0	0.1	1.0
10-24.9	0.0	0.0	0.3	0.0	0.3
>25	0.0	0.0	0.0	0.0	0.0
Late	2.0	1.8	16.6	0.4	20.9
<0.5	0.2	0.4	2.5	0.3	3.3
0.5-0.99	1.3	0.3	2.5	0.0	4.1
1-2.49	0.5	1.0	9.2	0.0	10.8
2.5-4.99	0.0	0.0	1.9	0.1	2.0
5-9.99	0.0	0.0	0.5	0.1	0.6
10-24.9	0.0	0.0	0.1	0.0	0.1
>25	0.0	0.0	0.0	0.0	0.0
Old-Growth	3.8	1.8	17.3	0.5	23.4
<0.5	1.8	1.2	3.1	0.0	6.1
0.5-0.99	0.4	0.5	5.2	0.0	6.2
1-2.49	1.2	0.1	7.3	0.3	8.9
2.5-4.99	0.3	0.0	1.3	0.2	1.8
5-9.99	0.0	0.0	0.3	0.0	0.3
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.1	0.0	0.1
All	12.2	16.2	69.4	2.2	100.0

Table A-2.12. Proportion of the silver fir vegetation zone in the Pacific Northwest by stage of structural development and mortality level classified into one of four trajectories of structural change based on changes density of trees per ha and quadratic mean diameter where: “densifying”: $\Delta TPH \geq 0$ and $\Delta QMD < 0$, “aggrading”: $\Delta TPH \geq 0$ and $\Delta QMD \geq 0$, “die-back”: $\Delta TPH < 0$ and $\Delta QMD < 0$, and “thinning”: $\Delta TPH < 0$ and $\Delta QMD > 0$.

Stage	Silver Fir				
	Densifying	Aggrading	Thinning	Die-back	All
Early	0.0	4.6	0.7	0.0	5.3
<0.5	0.0	2.8	0.0	0.0	2.8
0.5-0.99	0.0	0.8	0.0	0.0	0.8
1-2.49	0.0	1.0	0.7	0.0	1.7
2.5-4.99	0.0	0.0	0.0	0.0	0.0
5-9.99	0.0	0.0	0.0	0.0	0.0
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
Mid	1.3	7.3	3.2	0.0	11.8
<0.5	0.2	2.8	0.6	0.0	3.7
0.5-0.99	0.8	1.6	0.7	0.0	3.1
1-2.49	0.3	2.5	1.4	0.0	4.3
2.5-4.99	0.0	0.3	0.1	0.0	0.4
5-9.99	0.0	0.0	0.3	0.0	0.3
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
Mature	1.7	1.6	5.1	0.6	9.0
<0.5	0.9	0.5	0.8	0.0	2.1
0.5-0.99	0.3	0.4	0.9	0.0	1.6
1-2.49	0.5	0.7	2.9	0.0	4.1
2.5-4.99	0.0	0.0	0.5	0.6	1.1
5-9.99	0.1	0.0	0.0	0.0	0.1
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
Late	9.9	4.0	34.9	1.7	50.6
<0.5	3.3	1.5	3.2	0.1	8.1
0.5-0.99	2.0	0.4	6.7	0.1	9.2
1-2.49	4.3	1.5	17.0	0.6	23.4
2.5-4.99	0.4	0.6	6.2	0.6	7.9
5-9.99	0.0	0.0	1.4	0.0	1.4
10-24.9	0.0	0.0	0.3	0.0	0.3
>25	0.0	0.0	0.0	0.3	0.3
Old-Growth	7.1	1.4	13.0	1.8	23.3
<0.5	1.7	0.7	2.1	0.4	5.0
0.5-0.99	2.1	0.3	4.2	0.3	6.9
1-2.49	3.3	0.4	4.4	0.7	8.8
2.5-4.99	0.0	0.0	1.7	0.4	2.1
5-9.99	0.0	0.0	0.6	0.0	0.6
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
All	20.1	18.9	56.9	4.2	100.0

Table A-2.13. Proportion of the mountain hemlock vegetation zone in the Pacific Northwest by stage of structural development and mortality level classified into one of four trajectories of structural change based on changes density of trees per ha and quadratic mean diameter where: “densifying”: ΔTPH≥0 and ΔQMD <0, “aggrading”: ΔTPH ≥0 and ΔQMD ≥0, “die-back”: ΔTPH <0 and ΔQMD <0, and “thinning”: ΔTPH<0 and ΔQMD>0.

Stage	Mountain Hemlock				
	Densifying	Aggrading	Thinning	Die-back	All
Early	0.1	0.7	0.4	0.0	1.2
<0.5	0.0	0.4	0.4	0.0	0.8
0.5-0.99	0.1	0.1	0.0	0.0	0.2
1-2.49	0.0	0.2	0.0	0.0	0.2
2.5-4.99	0.0	0.0	0.0	0.0	0.0
5-9.99	0.0	0.0	0.0	0.0	0.0
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
Mid	0.9	1.1	2.0	0.0	4.1
<0.5	0.1	0.5	0.9	0.0	1.5
0.5-0.99	0.0	0.5	0.1	0.0	0.6
1-2.49	0.4	0.1	0.5	0.0	1.0
2.5-4.99	0.4	0.0	0.5	0.0	0.9
5-9.99	0.0	0.0	0.0	0.0	0.0
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
Mature	3.6	4.6	4.9	0.4	13.4
<0.5	2.0	1.6	0.4	0.0	4.1
0.5-0.99	1.1	1.8	1.4	0.0	4.4
1-2.49	0.4	1.0	1.6	0.0	3.1
2.5-4.99	0.0	0.1	1.0	0.0	1.1
5-9.99	0.0	0.0	0.4	0.4	0.8
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
Late	0.0	0.1	1.2	0.0	1.3
<0.5	0.0	0.1	0.1	0.0	0.2
0.5-0.99	0.0	0.0	0.1	0.0	0.1
1-2.49	0.0	0.0	0.6	0.0	0.6
2.5-4.99	0.0	0.0	0.4	0.0	0.4
5-9.99	0.0	0.0	0.0	0.0	0.0
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
Old-Growth	18.5	8.1	47.6	5.8	80.0
<0.5	7.8	2.4	8.0	0.5	18.8
0.5-0.99	6.5	4.7	9.6	1.2	22.0
1-2.49	3.8	1.0	22.0	1.7	28.5
2.5-4.99	0.4	0.0	6.3	1.8	8.5
5-9.99	0.0	0.0	1.2	0.1	1.3
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.4	0.4	0.8
All	23.0	14.6	56.1	6.2	100.0

Table A-2.14. Proportion of the subalpine vegetation zone in the Pacific Northwest by stage of structural development and mortality level classified into one of four trajectories of structural change based on changes density of trees per ha and quadratic mean diameter where: “densifying”: $\Delta TPH \geq 0$ and $\Delta QMD < 0$, “aggrading”: $\Delta TPH \geq 0$ and $\Delta QMD \geq 0$, “die-back”: $\Delta TPH < 0$ and $\Delta QMD < 0$, and “thinning”: $\Delta TPH < 0$ and $\Delta QMD > 0$.

Stage	Subalpine				
	Densifying	Aggrading	Thinning	Die-back	All
Early	1.1	1.2	0.0	0.0	2.2
<0.5	0.7	0.1	0.0	0.0	0.8
0.5-0.99	0.4	1.0	0.0	0.0	1.3
1-2.49	0.0	0.1	0.0	0.0	0.1
2.5-4.99	0.0	0.0	0.0	0.0	0.0
5-9.99	0.0	0.0	0.0	0.0	0.0
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
Mid	2.9	1.9	3.7	0.4	8.9
<0.5	1.7	1.2	1.6	0.0	4.5
0.5-0.99	0.4	0.8	0.1	0.0	1.2
1-2.49	0.8	0.0	0.9	0.4	2.0
2.5-4.99	0.0	0.0	0.3	0.0	0.3
5-9.99	0.0	0.0	0.0	0.0	0.0
10-24.9	0.0	0.0	0.1	0.0	0.1
>25	0.0	0.0	0.8	0.0	0.8
Mature	4.1	7.4	12.7	2.3	26.5
<0.5	1.8	4.4	2.1	0.0	8.3
0.5-0.99	1.3	2.6	1.2	0.0	5.2
1-2.49	1.0	0.4	6.3	0.0	7.7
2.5-4.99	0.0	0.0	2.0	1.2	3.2
5-9.99	0.0	0.0	0.9	0.8	1.6
10-24.9	0.0	0.0	0.1	0.0	0.1
>25	0.0	0.0	0.1	0.4	0.5
Late	0.9	0.1	6.0	1.4	8.4
<0.5	0.5	0.1	0.4	0.0	1.0
0.5-0.99	0.4	0.0	1.0	0.0	1.3
1-2.49	0.0	0.0	1.6	0.4	2.0
2.5-4.99	0.0	0.0	1.4	0.1	1.5
5-9.99	0.0	0.0	1.2	0.5	1.7
10-24.9	0.0	0.0	0.4	0.0	0.4
>25	0.0	0.0	0.0	0.5	0.5
Old-Growth	9.1	4.5	36.3	4.1	54.0
<0.5	3.4	2.5	3.8	0.0	9.8
0.5-0.99	2.1	1.0	6.8	0.0	9.9
1-2.49	2.8	1.1	13.3	0.2	17.3
2.5-4.99	0.8	0.0	7.3	1.5	9.6
5-9.99	0.0	0.0	2.1	0.4	2.5
10-24.9	0.0	0.0	2.3	0.8	3.1
>25	0.0	0.0	0.8	1.2	2.0
All	18.0	15.0	58.8	8.2	100.0

Table A-2.15. Proportion of the grand/white fir vegetation zone in the Pacific Northwest by stage of structural development and mortality level classified into one of four trajectories of structural change based on changes density of trees per ha and quadratic mean diameter where: “densifying”: ΔTPH≥0 and ΔQMD <0, “aggrading”: ΔTPH ≥0 and ΔQMD ≥0, “die-back”: ΔTPH <0 and ΔQMD <0, and “thinning”: ΔTPH<0 and ΔQMD>0.

Stage	Grand/White Fir				
	Densifying	Aggrading	Thinning	Die-back	All
Early	0.3	1.5	0.4	0.0	2.2
<0.5	0.1	1.2	0.0	0.0	1.4
0.5-0.99	0.0	0.1	0.2	0.0	0.2
1-2.49	0.2	0.2	0.1	0.0	0.4
2.5-4.99	0.0	0.0	0.2	0.0	0.2
5-9.99	0.0	0.0	0.0	0.0	0.0
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
Mid	3.4	3.5	5.4	0.6	12.9
<0.5	1.7	2.1	1.5	0.1	5.2
0.5-0.99	0.7	1.2	0.5	0.0	2.4
1-2.49	1.0	0.3	1.4	0.0	2.7
2.5-4.99	0.1	0.0	1.9	0.2	2.1
5-9.99	0.0	0.0	0.1	0.0	0.1
10-24.9	0.0	0.0	0.1	0.2	0.2
>25	0.0	0.0	0.0	0.2	0.2
Mature	5.4	4.8	7.5	0.4	18.1
<0.5	1.8	4.1	1.4	0.0	7.3
0.5-0.99	1.8	0.3	2.1	0.1	4.2
1-2.49	1.5	0.4	3.0	0.0	4.8
2.5-4.99	0.4	0.1	0.5	0.1	1.0
5-9.99	0.0	0.0	0.2	0.2	0.4
10-24.9	0.0	0.0	0.1	0.0	0.1
>25	0.0	0.0	0.4	0.1	0.4
Late	3.0	2.4	9.2	0.6	15.3
<0.5	1.1	1.6	1.2	0.0	3.8
0.5-0.99	0.4	0.4	1.6	0.0	2.3
1-2.49	1.2	0.5	3.7	0.1	5.4
2.5-4.99	0.4	0.0	1.8	0.3	2.5
5-9.99	0.0	0.0	0.7	0.1	0.8
10-24.9	0.0	0.0	0.1	0.1	0.1
>25	0.0	0.0	0.1	0.2	0.3
Old-Growth	12.0	4.7	31.8	3.0	51.5
<0.5	3.4	2.1	3.5	0.2	9.2
0.5-0.99	3.5	1.8	5.1	0.2	10.6
1-2.49	4.2	0.6	14.4	1.4	20.7
2.5-4.99	0.9	0.2	5.3	0.1	6.5
5-9.99	0.0	0.0	1.3	0.3	1.6
10-24.9	0.0	0.0	1.4	0.2	1.7
>25	0.0	0.0	0.7	0.6	1.3
All	24.2	16.9	54.3	4.6	100.0

Table A-2.16. Proportion of the Douglas-fir vegetation zone in the Pacific Northwest by stage of structural development and mortality level classified into one of four trajectories of structural change based on changes density of trees per ha and quadratic mean diameter where: “densifying”: $\Delta\text{TPH}\geq 0$ and $\Delta\text{QMD} < 0$, “aggrading”: $\Delta\text{TPH} \geq 0$ and $\Delta\text{QMD} \geq 0$, “die-back”: $\Delta\text{TPH} < 0$ and $\Delta\text{QMD} < 0$, and “thinning”: $\Delta\text{TPH} < 0$ and $\Delta\text{QMD} > 0$.

Stage	Douglas-fir				
	Densifying	Aggrading	Thinning	Die-back	All
Early	0.0	2.4	0.5	0.3	3.1
<0.5	0.0	2.1	0.0	0.0	2.1
0.5-0.99	0.0	0.3	0.0	0.0	0.3
1-2.49	0.0	0.0	0.4	0.0	0.4
2.5-4.99	0.0	0.0	0.0	0.0	0.0
5-9.99	0.0	0.0	0.0	0.0	0.0
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.1	0.3	0.4
Mid	2.0	3.6	7.7	0.8	14.1
<0.5	1.1	3.6	3.8	0.0	8.5
0.5-0.99	0.7	0.0	1.6	0.0	2.3
1-2.49	0.2	0.0	0.9	0.1	1.1
2.5-4.99	0.0	0.0	0.4	0.0	0.4
5-9.99	0.0	0.0	0.1	0.1	0.2
10-24.9	0.0	0.0	0.4	0.1	0.5
>25	0.0	0.0	0.6	0.6	1.2
Mature	5.4	7.3	19.2	1.0	33.0
<0.5	2.8	5.4	3.9	0.3	12.4
0.5-0.99	1.1	1.1	4.4	0.0	6.6
1-2.49	1.2	0.7	6.0	0.0	7.9
2.5-4.99	0.3	0.0	3.1	0.1	3.4
5-9.99	0.0	0.0	0.5	0.1	0.5
10-24.9	0.0	0.0	1.2	0.0	1.2
>25	0.0	0.0	0.3	0.6	0.9
Late	1.7	2.1	5.6	1.7	11.1
<0.5	0.2	2.1	1.0	0.0	3.3
0.5-0.99	0.2	0.0	0.9	0.0	1.0
1-2.49	0.9	0.0	1.1	0.4	2.4
2.5-4.99	0.4	0.0	1.3	0.0	1.7
5-9.99	0.0	0.0	0.3	0.1	0.4
10-24.9	0.1	0.0	0.9	0.3	1.3
>25	0.0	0.0	0.1	1.0	1.0
Old-Growth	4.2	5.4	27.2	2.0	38.8
<0.5	1.0	2.8	5.6	0.0	9.5
0.5-0.99	1.9	1.2	3.0	0.0	6.0
1-2.49	1.3	1.3	10.9	0.2	13.7
2.5-4.99	0.0	0.1	3.4	0.7	4.2
5-9.99	0.0	0.0	1.6	0.0	1.6
10-24.9	0.0	0.0	1.9	0.3	2.2
>25	0.0	0.0	0.7	0.9	1.6
All	13.4	20.7	60.1	5.9	100.0

Table A-2.17. Proportion of the ponderosa pine vegetation zone in the Pacific Northwest by stage of structural development and mortality level classified into one of four trajectories of structural change based on changes density of trees per ha and quadratic mean diameter where: “densifying”: ΔTPH≥0 and ΔQMD <0, “aggrading”: ΔTPH ≥0 and ΔQMD ≥0, “die-back”: ΔTPH <0 and ΔQMD <0, and “thinning”: ΔTPH<0 and ΔQMD>0.

Stage	Ponderosa Pine				
	Densifying	Aggrading	Thinning	Die-back	All
Early	0.1	1.3	1.6	0.0	3.0
<0.5	0.1	0.7	0.0	0.0	0.8
0.5-0.99	0.0	0.5	1.1	0.0	1.6
1-2.49	0.0	0.0	0.5	0.0	0.5
2.5-4.99	0.0	0.1	0.0	0.0	0.1
5-9.99	0.0	0.0	0.0	0.0	0.0
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.0	0.0	0.0
Mid	6.2	15.0	13.2	0.5	34.9
<0.5	4.1	11.7	4.4	0.0	20.2
0.5-0.99	0.3	1.1	1.7	0.0	3.0
1-2.49	1.8	2.2	4.7	0.0	8.8
2.5-4.99	0.0	0.0	2.0	0.0	2.0
5-9.99	0.0	0.0	0.3	0.0	0.3
10-24.9	0.0	0.0	0.1	0.0	0.1
>25	0.0	0.0	0.0	0.5	0.5
Mature	5.3	14.1	15.8	0.7	35.8
<0.5	3.3	12.1	6.6	0.0	22.0
0.5-0.99	0.3	2.0	3.4	0.1	5.8
1-2.49	1.7	0.0	2.9	0.0	4.6
2.5-4.99	0.0	0.0	2.1	0.0	2.1
5-9.99	0.0	0.0	0.3	0.0	0.3
10-24.9	0.0	0.0	0.5	0.0	0.5
>25	0.0	0.0	0.0	0.5	0.5
Late	1.5	1.8	9.4	1.2	13.8
<0.5	0.5	1.3	1.3	0.0	3.2
0.5-0.99	0.7	0.0	2.1	0.1	2.9
1-2.49	0.1	0.5	2.9	0.0	3.6
2.5-4.99	0.1	0.0	1.6	0.5	2.2
5-9.99	0.0	0.0	0.7	0.0	0.7
10-24.9	0.0	0.0	0.1	0.0	0.1
>25	0.0	0.0	0.7	0.5	1.2
Old-Growth	2.2	1.5	7.9	0.8	12.4
<0.5	1.2	0.3	0.8	0.0	2.2
0.5-0.99	1.1	0.7	1.8	0.3	3.8
1-2.49	0.0	0.5	1.8	0.0	2.4
2.5-4.99	0.0	0.0	2.4	0.0	2.4
5-9.99	0.0	0.0	0.5	0.5	1.1
10-24.9	0.0	0.0	0.0	0.0	0.0
>25	0.0	0.0	0.5	0.0	0.5
All	15.3	33.7	47.8	3.2	100.0